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**Evaluation of modeling ecosystem  
seasonality in the University of Victoria  
Earth System Climate Model**

**Focus: The phytoplankton spring bloom  
in the North Atlantic**

**Master thesis**

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## Abstract

Investigating climate model ability to simulate ecosystem seasonality, for instance causes and dynamics of phytoplankton blooms in the North Atlantic, is of major importance, because interannual and seasonal variations in bloom timing, duration and intensity caused by anthropogenic induced global climate change, can lead to species shifts and alterations in the trophic food web and biogeochemical cycles, which otherwise may remain undetected on an annual scale.

The seasonal variability of the North Atlantic spring bloom is highly related to surface  $p\text{CO}_2$  (Takahashi et al., 2002; Corbiere et al., 2007; Signorini et al., 2012) and bloom dynamics have a substantial role in carbon sequestration (Watson et al., 1991; Townsend et al., 1994). Hence it is necessary to improve predictions of seasonal variability in ecosystem models in order to simulate future global warming more precisely.

To evaluate the accuracy of the University of Victoria Earth System climate model (UVic model) simulations of timing, forcing factors and limitations (e.g. mixed layer depth, temperature, irradiance, nutrients, zooplankton grazing pressure) to the North Atlantic spring bloom, model output has been compared to observations from MODIS satellite images, WOA09 data, IFREMER records and PAP measurements.

The results showed that the UVic model simulated phytoplankton growth rates inaccurately and estimated the spring bloom start approximately one month too late. The model consistently underestimated actual temperature values, but temperature changes were significantly correlated between observations and predictions. The mixed layer shallowed earlier, more and patchier in practice than in the model. The simulated bloom is limited by solar radiance in early spring, while nutrient limitations are pivotal during summer. At specific study sites temperature was detected as driving factor for bloom formation. The role of the mixed layer depth on bloom dynamics was not simulated adequately by UVic.

Therefore especially simulations of the mixed layer depth and associated shoaling processes need to be optimized, maybe by improved parameterization of eddies and wind stress, to achieve accurate predictions of bloom dynamics and related forcing factors. This is important to provide precise simulations of phytoplankton bloom dynamics in the North Atlantic region for solid predictions about  $\text{CO}_2$  sequestration, biological pump magnitude and other biological and physical interaction processes with respect to seasonal variability.

## 1. Introduction

Earth System Climate Models are mathematical representations of global biogeochemical cycles and climate systems. They are used to investigate physical, biological and chemical interactions and have been developed to enable improved understanding of Earth's climate system and to explore anthropogenic induced alterations in future climate scenarios (Bagniewski et al., 2011).

In this study the ability of the University of Victoria Earth System Climate Model (UVic model) (Weaver et al., 2001; Eby et al., 2009; Keller et al., 2012) to reproduce satellite and field observations is evaluated. The incorporated ecosystem model was recently improved by Keller et al. (2012). One major modification is the optimized simulation of marine ecosystem seasonality at temperate and high latitudes and their influence on biogeochemical cycles. Whether the model predicts the causes of the simulated spring phytoplankton bloom in the North Atlantic region correctly has not been thoroughly assessed yet. It is also still unknown if ecosystem seasonality is important for simulating climate change and seasonal variations particularly in CO<sub>2</sub>-sequestration more accurately.

### 1.1. Phytoplankton bloom biology and seasonality

The oceans and marine ecosystems play a major role in the biogeochemical cycles of e.g. the key nutrients nitrogen and phosphorus. Both control phytoplankton growth, their reproduction as well as the magnitude of primary production and are thereby associated to the global carbon cycle, which is considered to be a major driver of climate change (Keller et al., 2012).

One contributor to carbon sequestration is the biological pump (Longhurst and Harrison, 1989), exporting carbon from the ocean's surface to the depth. Phytoplankton cells take up carbon biologically via photosynthesis in the sunlit layer and transfer the organic material mainly by sinking processes downwards to the bottom (Anderson, 2005; Keller et al., 2012). This process is influencing Earth's climate by decreasing atmospheric CO<sub>2</sub> levels and thereby reducing global warming effects (Longhurst and Harrison, 1989).

The effectiveness of the carbon pump depends on the ratio of particulate organic carbon (POC) to particulate inorganic carbon (PIC) in the transported material and thus controls the air-sea CO<sub>2</sub> flux (Signorini et al., 2012). The export of organic carbon is furthermore affected

by the particle's sinking rate, which in turn is determined by their buoyancy and shape (Bagniewski et al., 2011). It is estimated that this mechanism transports 5 – 20 Gt carbon per year from the sunlit layer into deeper zones (Henson et al., 2011).

Half of the global primary production stems from phytoplankton photosynthesis (Longhurst et al., 1995). This primary production is a major contributor to the oceanic uptake of CO<sub>2</sub> and its interannual and seasonal variability is highly related to surface *p*CO<sub>2</sub> (Corbiere et al., 2007; Signorini et al., 2012). CO<sub>2</sub> sequestration is particularly large at higher latitudes (< 30°N), like in the North Atlantic, where 25 % of global oceanic uptake of anthropogenic carbon is presumed (Takahashi et al., 2009), with the spring bloom being a key component of this uptake (Bagniewski et al., 2011).

Thus, phytoplankton populations have a considerable impact on carbon sequestration at a regional and global scale (Longhurst and Harrison, 1989), especially the seasonally occurring phytoplankton spring bloom (Martinez et al., 2011). The distribution of blooms has also been linked to the concentration of inorganic carbon, sea surface temperature and the partial pressure of CO<sub>2</sub> in the water column (Watson et al., 1991; Lochte et al., 1993).

Nonetheless main contributor to carbon uptake is the so called solubility pump and the deep water formation in the North Atlantic region, together leading to a net CO<sub>2</sub> uptake of 20% (Takahashi et al., 2002; Sabine et al., 2004).

In addition to their biogeochemical influence, phytoplankton blooms are also prominent components of pelagic food webs and propagate bottom-up controls to higher trophic levels (Richardson and Schoeman, 2004). The development of phytoplankton blooms is correlated with life cycles of larval fish and zooplankton (Platt et al., 2003). Their survival rates are highly dependent on phytoplankton bloom dynamics, since in the marine realm they are the food basis for other trophic levels, i.e. from grazers to top predators (Cushing, 1990). The onset of a bloom formation could be affected by a changing climate, which may lead to a temporal mismatch of phytoplankton bloom and larval hatching (Cushing, 1990). The reduced life cycle synchrony may lead to a higher larval mortality rate, and can, next to other factors, substantially influence recruitment processes in fish population dynamics (Edwards and Richardson, 2004). Therefore it is of major importance to study causes and consequences of phytoplankton blooms and their interannual and seasonal variation in coincidence with anthropogenic induced climate alterations (Brody et al., 2013).

A phytoplankton bloom is characterized by large abundances of phytoplankton cells in the surface layers of the ocean, resulting from a period of high population growth rates (Martinez et al., 2011). The increase of phytoplankton biomass is referred to as spring or vernal bloom, when it occurs in temperate regions during spring (Mann and Lazier, 2006).

At higher latitudes phytoplankton blooms are seasonal events and their development is controlled by special abiotic factors like solar radiation and temperature which contribute to the stratification of the water column. In the transition zone, between the subpolar and subtropical gyre, the first and main phytoplankton peak arises during spring, and the second smaller one in fall (D'Ortenzio et al., 2012), determined by the interplay of nutrients and light conditions (Henson et al., 2009). Further north, light increasingly becomes the limiting factor, resulting in one main bloom in spring or summer (Henson et al., 2009; Brody et al., 2013). This study focuses on the initiation of the phytoplankton bloom during spring in the North Atlantic region 30°-70°N 60°-10° W.

### ***1.1.1. Initiation of phytoplankton blooms***

To assess the various abiotic and biotic factors, like for instance light availability, nutrient accessibility, zooplankton grazing pressure, deep turbulent mixing in winter and the subsequent spring stratification (Nanninga and Tyrrell, 1996), is important when analyzing the causes of phytoplankton bloom formations. Previous studies proposed different hypotheses to explain this context.

First, the rise in irradiance during spring was thought to trigger the spring bloom (Atkins, 1928), since phytoplankton cells need sufficient light conditions to perform photosynthesis and increase their growth rates. The photosynthetic rate decreases with depth, proportional to the intensity of radiation. So the ocean layer offering a proper level of solar radiation to enable photosynthesis by phytoplankton cells is called the euphotic zone.

In the study area wind stress and the consequent convection of cold water at the ocean's surface are reasons for a nearly complete mixing of the water column in late winter (Mann and Lazier, 2006). This deep mixing as well as the low solar radiation during winter caused by low sun angles, limit phytoplankton population growth rates.

### ***1.1.2. Sverdrup Hypothesis***

The most cited theory about spring bloom development is the Critical-Depth-Hypothesis of Sverdrup (1953). He assumed phytoplankton cells to be circulated and homogeneously distributed in the water column due to turbulence induced vertical mixing, down to the maximum depth of the mixed layer.

The mixed layer depth is the depth, where the water density difference to the surface is  $0.01\rho$  and more (Bagniewski et al., 2011) or else where the temperature difference to 10m depth is  $0.2^{\circ}\text{C}$  (Martinez et al., 2011). The mixed layer depth varies diurnally and seasonally depending on the solar radiation budget and thereby on the air-sea heat fluxes (Wolf and Woods, 1988; Lochte et al., 1993).

Concomitantly with depth the production rate of phytoplankton decreases logarithmically. The respiration rate exceeds the photosynthetic rate near the bottom (Mann and Lazier, 2006), while the opposite is true for surface waters. The depth, where the rates of photosynthesis and respiration equal is called compensation depth ( $D_c$ ). A rise in phytoplankton biomass occurs when integrated respiration levels are lower than integrated production levels. The depth, where integrated respiration is balanced by integrated production is called the critical depth of the mixed layer (Brody et al., 2013). The extent of the mixed layer in relation to the critical depth determines the overall increase or decrease of phytoplankton biomass.

The shallower the depth of the mixed layer is in relation to the critical depth the higher is the planktonic growth rate (Mann and Lazier, 2006). Phytoplankton populations grow within the surface mixed layer when the mixed layer is shallow and their overall net primary production is positive (Bagniewski et al., 2011).

Gran and Braarud (1935) stated that a major factor influencing the growth of phytoplankton and their primary production is the “stabilization of the water column by thermal stratification”. The surface warming of the water by absorbing incoming short-wave radiation causes stratification (Mann and Lazier, 2006), which is a process that establishes separated water layers with distinct characteristics.

Due to sharp gradients in temperature or density, the vertical mixing from the lighter upper layer to the denser lower layer is suppressed, because this thermocline or pycnocline is a natural barrier between both water masses (Mann and Lazier, 2006).



Sverdrup (1953) assumed stratification as well as sufficient light and nutrients to be the factors initiating a spring bloom. Stratification and a shallower mixing depth cause phytoplankton to stay longer in the upper layer under favorable conditions, since more light and nutrients are available here in the beginning of spring. Thus phytoplankton cells have higher photosynthetic rates, so that the net primary production exceeds respiration and consequently stimulating their growth leading to a phytoplankton bloom (Sverdrup, 1953; Bagniewski et al., 2011; Brody et al., 2013).

The presence of a spring bloom is, however, not only controlled by light, temperature and mixed layer conditions, but also by ambient nutrient levels. The aforementioned mechanism brings nutrients from great depths to the surface.

The nitrate concentration in the upper layer rises during winter deep mixing (Mann and Lazier, 2006), mainly due to the entrainment of waters with a high remineralized nutrient content and lower consumption rates because phytoplankton populations are light-limited and do not use up the available nutrients. The shoaling of the mixed layer due to warming leads to a bloom during spring in the North Atlantic region. The increase in phytoplankton population size causes a fast depletion of nitrate in the surface ocean, which in turn restricts the population growth. Since the pycnocline limits the diffusion, virtually no new nutrients are entrained to the surface layer during summer, except what is regenerated by bacteria of the planktonic community. The process when phytoplankton cells use recycled nitrogen is called regenerated production. The ratio of total primary production of phytoplankton cells to new production, performed with nitrate entrained from below, is important for the global carbon cycle (Mann and Lazier, 2006).

In fall the cooling of the surface water and the limitation of solar irradiance, at higher latitudes due to shorter days, as well as convection processes and alternated wind stress deepen the mixed layer. During these turbulences nitrate and other nutrients are replenished to the surface waters from further down (Mann and Lazier, 2006).

The first bloom in early spring is usually formed by diatoms. Lampitt (1985) discovered that diatoms form large fast-sinking chain aggregates when the bloom phase declines which makes them to a key vector in exporting carbon to the deep ocean. Mesocosm experiments (Egge and Aksnes, 1992) and culture competition experiments (Sommer, 1994) discovered that diatoms

are dependent on a high silicate to nitrate ratio. Because silicate is, in contrast to nitrate, not regenerated in the shallow mixed layer during spring and cannot be renewed from deeper down, as vertical diffusion is missing due to the pycnocline, diatom bloom ends with silicate exhaustion.

At the end of spring the phytoplankton bloom can be terminated by different factors, such as grazing pressure by heterotrophs or exhaustion of nutrients (Banse, 1992, 2002; Signorini et al., 2012), which is affected among others by species competition (Ross and Sharples, 2011). Also viral infection can cause the lysis of phytoplankton cells (Baudoux et al., 2006) and other environmental factors can have an influence on phytoplankton survival and species composition as well.

The consumption by zooplankton and their excretion leads to a fast nitrogen reduction in the sunlit layer (Mann and Lazier, 2006). The consequence is a change in phytoplankton community composition. Subsequent blooms are mainly composed of dinoflagellates and coccolithophores (Signorini et al., 2012). Under low silicate to nitrate conditions sundry flagellates exhibit enhanced growth rates as they are able to migrate on a small scale to locations with higher nutrient concentrations (Mann and Lazier, 2006; Signorini et al., 2012). Coccolithophore blooms form, under advantageous solar irradiance, in late summer and by their production of calcite they alternate the amount of particulate organic carbon in the water column (Holligan et al., 1993a; Holligan et al., 1993b). At the end of summer, when the mixed layer depth increases and solar radiation budgets are reduced, chlorophyll *a* concentrations decrease significantly (Signorini et al., 2012).

This explanation of a bloom formation following the Critical-Depth-Hypothesis probably applies for light-limited sites at middle and high latitudes, located in the North Atlantic or western North Pacific (Mann and Lazier, 2006; Brody et al., 2013). However, regions of the North Pacific or the Southern Ocean do not show the development of a phytoplankton bloom in spring, although the water column is well stratified.

Doubts to Sverdrup's hypothesis do moreover exist because phytoplankton populations have been observed to start growing and developing a significant bloom before or even without an apparent vertical stratification of the surface layer (Townsend et al., 1992; Backhaus et al., 1999; Behrenfeld, 2010).

### ***1.1.3. Dilution-Recoupling Hypothesis***

Although maximum phytoplankton abundances correlate with shallow mixed layers and prior increases are linked to solar radiation, evidence that net growth rates act similarly is lacking. Therefore Behrenfeld (2010) formulated the Dilution-Recoupling-Hypothesis, which takes the interaction of phytoplankton growth and zooplankton grazing pressure as well as the seasonal changing of environmental conditions more into account. He claimed that the initiation of phytoplankton blooms takes place during winter, when the mixed layer depth is at the maximum and phytoplankton is diluted by vertical mixing. This dilution yields lower zooplankton grazing pressure and therefore enhances phytoplankton growth. The recoupling of algae growth and zooplankton grazing increases during spring. Behrenfelds study also argues that the growth increase starts though the depth of mixing still rise and before enhanced solar radiation is available. The hypothesis is based on the assumption that the annual bloom results from a decoupling of algae growth and losses (Banse, 2002).

The interactions between grazers and phytoplankton, however still need supplementary investigations to understand their annual cycle. Furthermore, the mechanism hypothesized by Behrenfeld has not been observed during the North Atlantic Bloom Experiment (NABE), because it was undertaken during a shallow mixed layer depth (Mahadevan et al., 2012). The NABE has been carried out at 47°N and 20°W in the years 1989 and 2008 as part of the Joint Global Ocean Flux Study (JGOFS) to observe phytoplankton dynamics, bloom development and related biogeochemical cycles in the North Atlantic (Ducklow, 1989; Dam et al., 1993; Lochte et al., 1993). During the experiment, the enhancement of chlorophyll began in spite of negative heat fluxes (Mahadevan et al., 2012), indicating that not solar heating, but eddy-driven restratification due to changes in the mixed layer depth and horizontal density gradients caused the bloom.

### ***1.1.4. The Role of Ocean Fronts and Eddies***

Eddies are formed by instabilities in the range of 1 to 10km that originate from horizontal density differences. Cyclonic eddies promote a bloom by yielding a vertical stratification of the water column by transporting denser water downwards from the north to south and in turn shifting lighter seawater northwards and up in the water column (Fig. 1). During this process a

spring bloom can occur prior to blooms caused by surface water warming, as described by model simulations (Mahadevan et al., 2012). This mechanism is counteracted by a cooling of the upper layer due to wind stress and convective mixing of the water column. Both processes determine the depth of the mixed layer and influence the bloom initiation and properties at middle to high latitudes of the North Atlantic. Without eddy formation shallowing of the mixed layer and bloom formation may occur 20-30 days later (Mahadevan et al., 2012). Satellite data of chlorophyll *a* as well as model simulations imply that the patchy distribution of the spring blooms is caused by eddies (Watson et al., 1991).

In addition to eddies, recent studies discovered a possible impact of ocean fronts on phytoplankton growth dynamics. The research of Taylor and Ferrari (2011) deals with ocean fronts, which are formed due to a gradient in temperature at horizontal scale. At oceanographic fronts stratification of the surface layer prevails, even if wind stress and consequent surface heat loss occurs (Fox-Kemper et al., 2008; Thomas and Taylor, 2010), thus phytoplankton cells are entrained in the euphotic zone (Taylor and Ferrari, 2011). Using MODIS Aqua satellite data, fronts could be identified as extremely productive areas. Chlorophyll *a* concentrations are highest at the front, indicating that local processes are likely the reason for enhanced phytoplankton growth. The authors theorize that a dynamic front, possibly including eddies, is a biological hotspot and promotes the development of patchy phytoplankton blooms. Especially at higher latitudes these processes can have an influence on the magnitude of the biological pump and future climate change, because of enhanced productivity by phytoplankton blooms (Lévy, 2005; Taylor and Ferrari, 2011). In subpolar regions this will contribute to stronger CO<sub>2</sub> sequestration, when vertical mixing at fronts diminishes and phytoplankton growth rates hence increase earlier. Therefore it is important to parameterize these processes in climate ecosystem models.

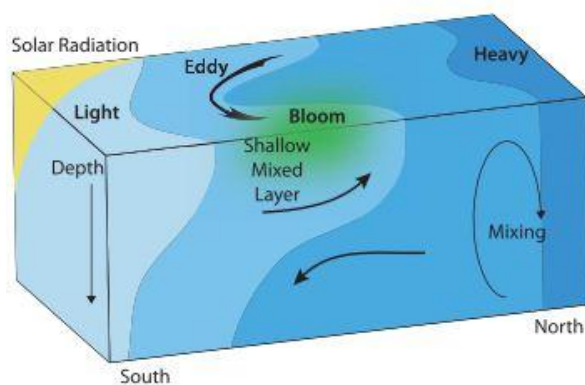


Figure 1: Resulting from winter deep mixing, upper ocean layers are denser to the north in spring. Eddies generate shallow mixed layer patches by moving lighter water upward and north and heavier water downward and south. By this process phytoplankton cells remain in the upper water layer and from the spring bloom. (Graphic by K. Mahadevan, 2012)

## **1.2. Modeling the phytoplankton spring bloom**

To simulate the North Atlantic spring bloom properly, the related variables and forcing factors, as described in previous sections, have to be parameterized accurate to reproduce observations correctly. If this is the case in the UVic model is the subject of this study.

The UVic model is a model of intermediate complexity (EMIC). Model types like this are used to investigate climate dynamics over long time periods. The more complex a model is the greater is the calculation effort and the needed processing power (Yool et al., 2011). Therefore EMIC's include climatic processes and mechanisms in a parameterized form, so that they are simple and feasible enough to conduct also long-term simulations (Claussen et al., 2002), which are important to ascertain future changes in Earth's climate.

In this examination phytoplankton is simulated in a simple nutrient – phytoplankton – zooplankton – detritus model, called NPZD model. The use of these four variables facilitates to keep model complexity simple but offering at the same time a required relation to reality (Heinle and Slawig, 2013). But recent approaches exist to develop NPZD models with higher complexity, by including e.g. different plant functional types or plankton size as well as biogeochemical cycles of iron and silicon (Yool et al., 2011). This could be important for better predicting algae bloom dynamics, as the timing, duration or development of spring phytoplankton blooms.

To identify when the bloom starts, it is pivotal to discover factors that force phytoplankton populations to grow and to form a bloom. The initiation of the bloom can either be identified as time where phytoplankton biomass crosses a set threshold or when population growth rates are highest (Brody et al., 2013). The method used will have influence on the defined bloom timing and on the analysis of potential drivers. Concerning the modeling of phytoplankton blooms, it is important how phytoplankton life cycles and variations of related variables are parameterized in models.

## 2. Aims of the Project

The aim of this project is to evaluate the ability of the University of Victoria Earth System climate model (UVic) to simulate timing and forcing factors of the North Atlantic spring bloom. The major questions of this thesis are:

Does the model correctly predict the timing of the bloom and what determines and sets off the bloom? What are the roles of temperature, mixed layer depth, irradiance, nutrients and zooplankton in controlling the simulated spring bloom? Does the model simulate the spring bloom at the right time, but for the wrong reasons?

Here it is hypothesized that the model correctly predicts the timing and location of the spring bloom and the related factors that have been identified as potential initiators or terminators (i.e. temperature, mixed layer depth, irradiance, nutrients, zooplankton grazing) of the bloom (e.g. Sverdrup, 1953; Martinez et al., 2011; Taylor and Ferrari, 2011). In this work the drivers that control the simulated spring bloom are analyzed, although there is still a controversial discussion in the scientific community (e.g. Behrenfeld, 2010; Mahadevan et al., 2012) about the environmental factors that initiate a spring bloom.

Answering the above questions may be important for a better understanding if simulating ecosystem seasonality, especially the North Atlantic spring bloom, is essential, because its seasonal variability is highly related to surface  $p\text{CO}_2$  (Corbiere et al., 2007; Signorini et al., 2012). In this context, the questions of whether future models should include seasonality and phytoplankton blooms in their climate simulations and connections of spring bloom seasonality and climate change are discussed.

### 3. Methods

#### 3.1. Study area: North Atlantic

The examined region in this study is the northern part of the North Atlantic (30°-70°N 60°-10°W) (Fig. 2), because the phytoplankton spring bloom is most pronounced here (Yoder et al., 1993) and has a crucial influence on the atmospheric carbon budget. The relatively heterogeneous region has been object to many studies on phytoplankton bloom development. Several research cruises and mooring stations have collected water samples and observations by satellite data are common.

The North Atlantic plays an important role in the global thermohaline circulation, which is also referred to as meridional overturning circulation. Driven by density differences, due to temperature and salinity gradients, the North Atlantic basin is mainly influenced by the Gulf Stream. Warm water masses, entering from the south, stream northwards and experience a cooling at the surface. The Labrador Sea as well as the region between Iceland, Greenland and Norway are areas of convection. In these regions ocean water sinks downwards to flow as North Atlantic Deep Water (NADW) to the south again (Rahmstorf, 1996) and they are important CO<sub>2</sub> sink locations. Approximately 5 to 10%, at high latitudes (>42°N) 0.2 – 0.5 Gt, of annual anthropogenic CO<sub>2</sub> emissions are sequestered to the deep ocean by the meridional overturning circulation (Takahashi et al., 1995) and thereby playing a major role in oceanic biogeochemical cycles and future climate change. The region is furthermore affected by varying sea ice cover on Greenland's eastern coast (Signorini et al., 2012), which also influences CO<sub>2</sub> uptake rates and the formation of phytoplankton blooms.

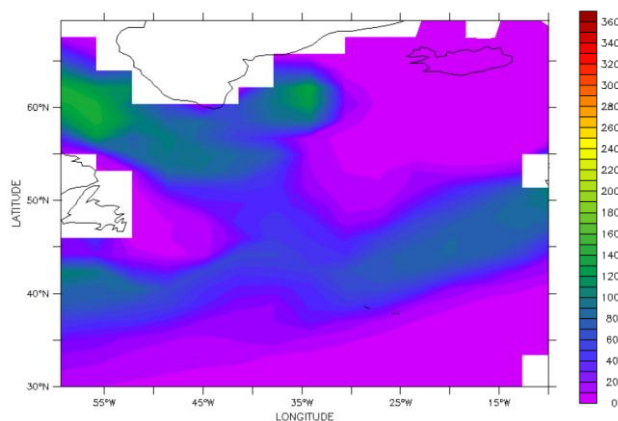


Figure 2: Phytoplankton biomass (mg C/m<sup>3</sup>) in the North Atlantic study region (30°-70°N 60°-10°W) during spring (April-May) simulated by the UVic model.

### 3.2. The UVic model

The evaluated model is the University of Victoria Earth System Climate model (UVic) of intermediate complexity (Eby et al., 2009) version 2.9 with modifications to the biogeochemical model by Keller et al. (2012). It is made up of three main components (Weaver et al., 2001) with  $3.6^\circ$  longitude  $\times$   $1.8^\circ$  latitude horizontal resolution, respectively. The first component contains a dynamic sea-ice model, the marine biogeochemical ecosystem model and a 3-D ocean circulation model (Modular Ocean Model 2) with parameterizations for tracer advection (Gent and Mc Williams, 1990), diffusive mixing across and along isopycnals, and diapycnal mixing tidally generated over rough countryside (Simmons et al., 2004). The second component is a modified terrestrial vegetation and carbon cycle model (Meissner et al., 2003) based on the Hadley Center model TRIFFID, which includes continental ice sheets that are held constant in the simulation. The third component is a one layer atmospheric energy-moisture balance model (Weaver et al., 2001).

The UVic model is forced by prescribed monthly climatological wind fields and historical CO<sub>2</sub> emissions. UVic does not simulate any interannual variability or eddies neither in the ocean nor in the atmosphere. The model is run for the year 2005.

The biogeochemical ecosystem model (Fig. 3) is a NPZD model (Schmittner et al., 2008) and modified by Keller et al. (2012). It consists of seven parameters including phosphate (PO<sub>4</sub>), nitrogen (NO<sub>3</sub>), oxygen (O<sub>2</sub>), nitrogen fixing phytoplankton (P<sub>D</sub>) and other phytoplankton (P<sub>O</sub>) as well as zooplankton (Z) and particulate detritus (D).

The non-diazotrophic phytoplankton growth rate ( $J_O$ ) is controlled by nitrogen and phosphate concentrations as well as by irradiance ( $I$ ) according to the following equations (Eq. 1, 2).

$$(1) \quad J_O = \min \left( J_{OI}, J_O^{\max} \cdot \frac{NO_3}{k_N + NO_3}, J_O^{\max} \cdot \frac{PO_4}{k_P + PO_4} \right)$$

$$(2) \quad J_{(O \text{ or } D)I} = \frac{J_{(O \text{ or } D)}^{\max} \alpha I}{\left[ (J_{(O \text{ or } D)}^{\max})^2 + (\alpha I)^2 \right]^{1/2}}$$



The growth rate of phytoplankton is dependent on temperature in the UVic model. At 0°C a maximum growth rate of 0.6 per day is used, according to previous studies about algae growth rates (Le Quéré et al., 2005; Keller et al., 2012).

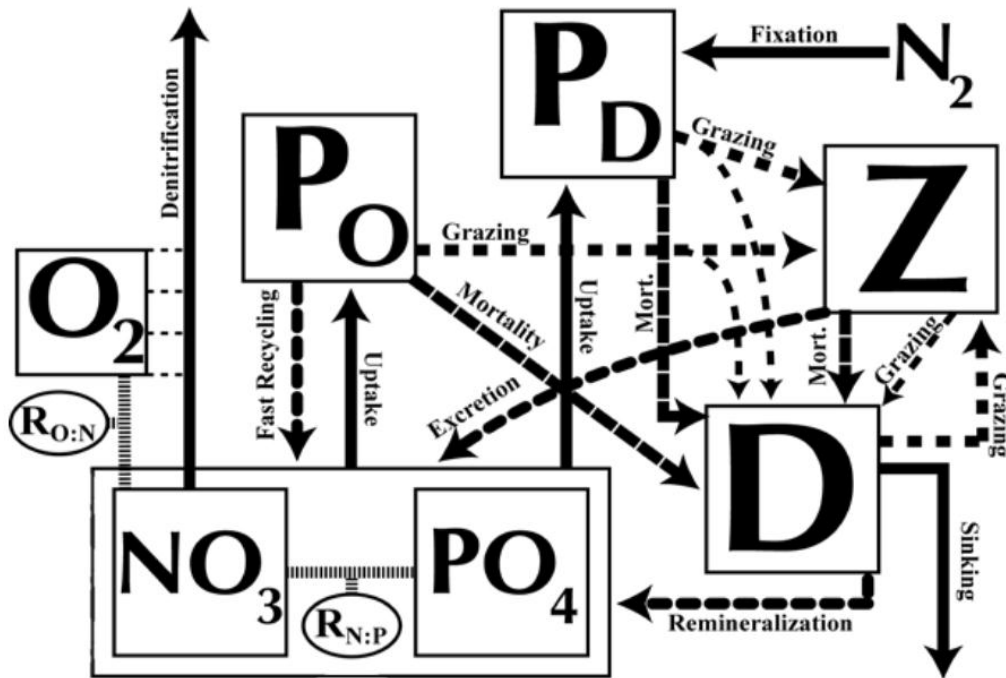


Figure 3: Schematic illustration of UVic ecosystem model visualizing model parameters (squares) and related material fluxes (arrows). (Keller et al., 2012)

### 3.3. Defining the bloom start date (BSD)

Two different methods are used to determine the bloom start date (BSD) (Brody et al., 2013) of the chlorophyll *a* data at the Porcupine Abyssal Plain-Eurosite station (PAP) (49°N 16.5°W; <http://www.eurosites.info>) averaged over the years 2003-2012 as well as of phytoplankton biomass at the UVic grid cell (49.5°N 16.2°W) nearest to this site.

In this study measured chlorophyll *a* concentrations are not converted to phytoplankton biomass, since the purpose of this study is to compare the timing and progression, not the actual magnitude in the context of displaying phytoplankton bloom development.

The first method investigates bloom commencement by analyzing when phytoplankton biomass or chlorophyll *a* concentration crosses a certain threshold (Siegel et al., 2002a; Henson et al., 2009; Cole et al., 2012; Brody et al., 2013). The so called threshold method describes the bloom start as date when chlorophyll *a* concentration or phytoplankton biomass

excesses the set threshold, defined as the median plus 5%, like in former studies (Henson et al., 2009; Cole et al., 2012; Brody et al., 2013). This method has been used in several studies to detect the timing of a phytoplankton bloom at basin and global scale in combination with ocean color data (Brody et al., 2013).

The second method defines bloom initiation as the date where the relative increase of chlorophyll *a* concentration or phytoplankton biomass is most rapid (Sharples et al., 2006; Brody et al., 2013). The bloom start date is therefore the first maximum of  $dchl/dt$  before the bloom peaks. This rate of change method is valuable for investigating seasonal biological or physical mechanisms that generate an environment which causes a spring bloom (Behrenfeld, 2010; Brody et al., 2013).

### **3.4. Comparing UVic simulations with observations**

For evaluating the model skill to simulate observations, monthly averaged measurements of chlorophyll *a* concentration, sea temperature and sea salinity at the PAP station, are compared to the UVic output.

To analyze if the model predicts timing and development of the North Atlantic spring bloom correctly, the model parameter phytoplankton biomass is compared with NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) monthly climatology satellite data of chlorophyll *a* concentration averaged over the years 2002-2013 (<http://modis.gsfc.nasa.gov>). Additionally ocean temperature data of World Ocean Atlas 2009 (WOA09) ([http://www.nodc.noaa.gov/OC5/WOA09/netcdf\\_data.html](http://www.nodc.noaa.gov/OC5/WOA09/netcdf_data.html)), which represents in situ parameters of 1° grid climatology fields, and their difference between prediction and observation, called misfit (Evans, 2003), has been analyzed to investigate the ability of the model to reproduce these data. Also data about the mixed layer depth ascertained by IFREMER, the French Research Institute for Exploration of the Sea (<http://www.ifremer.fr/cerweb/deboyer/mld/Data.php>) has been compared to the modeled mixed layer depth.

Chlorophyll *a* concentrations of MODIS are picturing the ocean's surface, while phytoplankton biomass of UVic is averaged over the first 50 meters. Here attention is drawn at the timing and development of the bloom, not the actual magnitude of it. Therefore only

timing differences in the development are detected in this examination and chlorophyll *a* data has not been converted to phytoplankton biomass.

Nonetheless the phytoplankton biomass has been converted from mol N/m<sup>3</sup> to mg C/m<sup>3</sup> using the Redfield ratio C:N 106:16=6,625 as to be consistent with previous studies (Redfield, 1934).

To statistically and graphically compare differences between the UVic simulation and observations the data sets are regridded onto the model grid in the Ferret software via linear interpolation (@FLN), except the measured data of the PAP station, which are compared to the named UVic grid cell. Also Matlab and Excel software are utilized for this examination.

In order to assess model skill the quantitative metrics described by Stow et al. (2003, 2009) are used. In the following equations  $n$  = number of observations,  $P_i$  = the  $i$ th of  $n$  predictions,  $\bar{P}$  = prediction averages,  $O_i$  = the  $i$ th of  $n$  observations and  $\bar{O}$  = observation averages.

For examining if the value of model predictions and observation data varies together the correlation coefficient  $r$  is used (Eq. 3).

$$(3) \quad r = \frac{\sum_{i=1}^n (O_i - \bar{O})(P_i - \bar{P})}{\sqrt{\sum_{i=1}^n (O_i - \bar{O})^2 \sum_{i=1}^n (P_i - \bar{P})^2}}$$

The correctness of the model simulations is investigated with the indices root mean squared error  $RMSE$ , average error  $AE$  and average absolute error  $AAE$  (Eq. 4-6).

$$(4) \quad RMSE = \sqrt{\frac{\sum_{i=1}^n (P_i - O_i)^2}{n}}$$

$$(5) \quad AE = \frac{\sum_{i=1}^n (P_i - O_i)}{n} = \bar{P} - \bar{O}$$

$$(6) \quad AAE = \frac{\sum_{i=1}^n |P_i - O_i|}{n}$$

The reliability index  $RI$  (Leggett and Williams, 1981) is used to calculate the factor by which predicted and observed values differ (Eq. 7).

$$(7) \quad RI = \exp \sqrt{\frac{1}{n} \sum_{i=1}^n \left( \log \frac{O_i}{P_i} \right)^2}$$

To evaluate how accurate model simulations can display observations the modeling efficiency  $MEF$  (Nash and Sutcliffe, 1970; Loague and Green, 1991) is calculated (Eq. 8).

$$(8) \quad MEF = \frac{\left( \sum_{i=1}^n (O_i - \bar{O})^2 - \sum_{i=1}^n (P_i - O_i)^2 \right)}{\sum_{i=1}^n (O_i - \bar{O})^2}$$

### 3.5. Analyzing potential factors causing the simulated spring bloom

To discover what is triggering the spring bloom in the UVic Earth System Climate Model correlations between phytoplankton biomass and the related parameters, such as temperature, mixed layer depth, nutrient concentrations, and zooplankton grazing pressure were done. Additionally potential limiting factors, as irradiance, nitrogen and phosphate, which could suppress phytoplankton growth rates, are analyzed. Furthermore the correlation coefficient  $r$  and the standard deviation  $\sigma$  for each parameter by averaging the simulated data points of every month at 49°N 16°W has been assessed using the Ferret correlation computation.

## 4. Results

### 4.1. Defining the bloom start date (BSD)

The bloom peak is defined as the date where phytoplankton or chlorophyll *a* concentrations reach a maximum value (Cole et al., 2012). The UVic model simulation displayed the first bloom peak to occur on May 23<sup>th</sup> at 49°N 16°W, with a value of 274.74 mg C/m<sup>3</sup>, 25 days later than observed by the PAP station, where the chlorophyll *a* concentration reached a maximum of 1.22 µg/L on April 28<sup>th</sup> (Fig. 4).

According to the threshold method the simulated UVic bloom began at 8<sup>th</sup> May with a phytoplankton biomass of 45.35 mg C/m<sup>3</sup> (threshold: 14.53 mg C/m<sup>3</sup>), while the observed bloom started 35 days earlier at April 3<sup>rd</sup> with a chlorophyll *a* concentration of 0.84 µg/L (threshold: 0.697 µg/L).

In contrast, the rate of change method defined the predicted bloom start date in the UVic model to be between May 13<sup>th</sup> and 18<sup>th</sup> with a rate of change of 101.77 mg C/m<sup>3</sup> per five days, but the observations at the PAP site postulated the bloom initiation to be at March 29<sup>th</sup> to April 3<sup>rd</sup> with a rate of change of 0.158 µg/L per five days, so 45 days earlier.

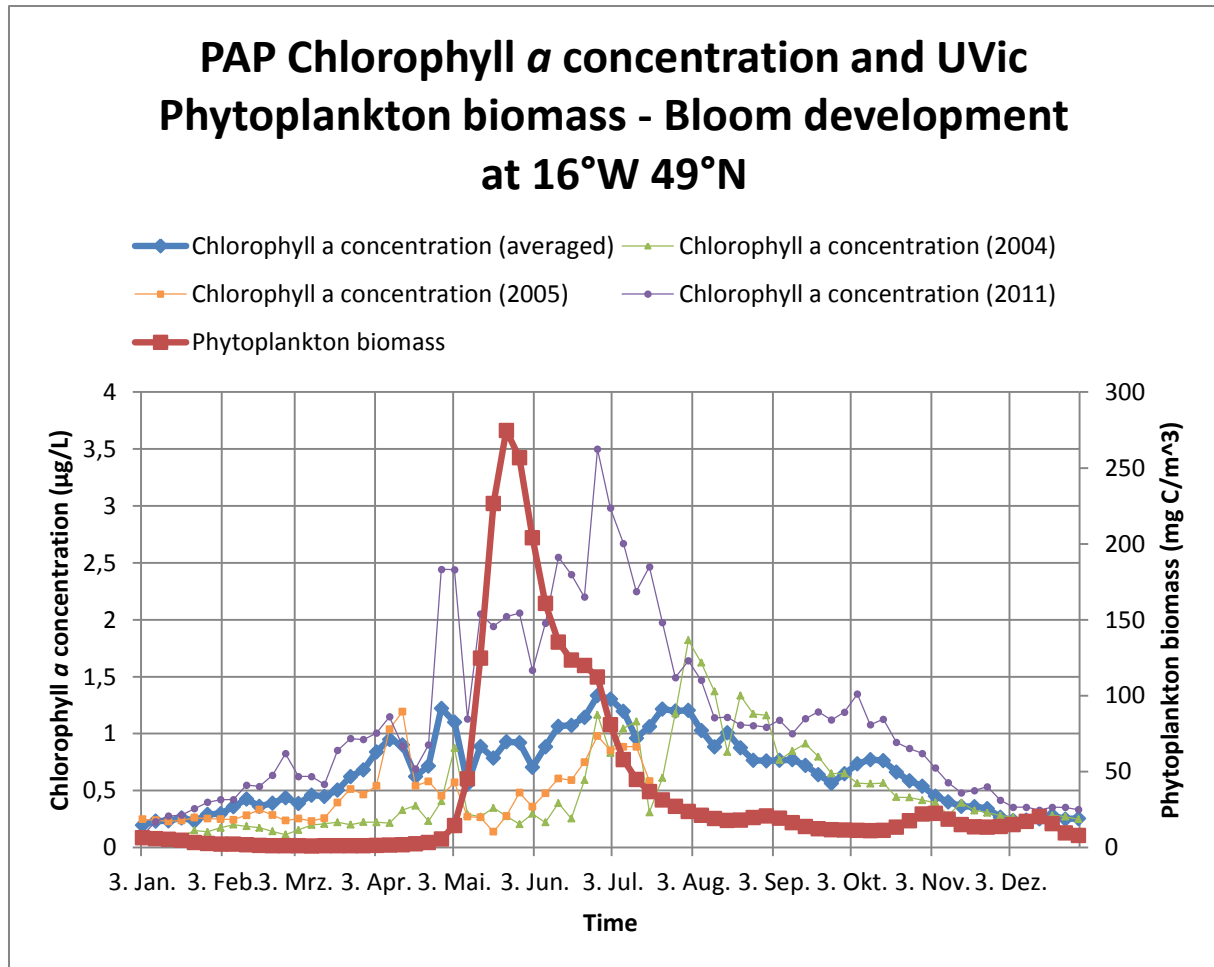


Figure 4: Chlorophyll  $a$  concentration ( $\mu\text{g/L}$ ) measured by PAP Eurosite averaged (blue diamonds) and for the years 2004, 2005 and 2011 as well as the UVic ocean phytoplankton biomass ( $\text{mg C/m}^3$ ) prediction (red squares) over time (days), at 49°N 16°W in the North Atlantic with data points every 5<sup>th</sup> day.

## 4.2. Comparison of UVic simulations and observations

To evaluate the UVic model skill to simulate properties such as phytoplankton biomass, temperature, sea water salinity and the mixed layer depth, in a specific region of the North Atlantic (30°-70°N 60°-10°W) and at a certain site (49°N 16°W), the mentioned quantitative metrics and graphical comparisons are analyzed in this section (described in section: 3. Methods).

#### 4.2.1. Comparison of PAP Chlorophyll *a* and UVic Phytoplankton biomass

By comparing PAP chlorophyll *a* measurements with UVic phytoplankton estimations the variation of both values had been analyzed (Fig. 5). The chlorophyll *a* concentration in the water column consistently increased on average from month to month. Nonetheless chlorophyll *a* concentrations are highly variable in every month and between every year (Fig. 4). The simulated phytoplankton biomass was predicted to be very low during February, March and April while a steep increase from April to May was expected, with high values in May and June whereas the content in July was decreasing. From April to May the simulated phytoplankton biomass increased by about 5643%, whereas the observed chlorophyll *a* concentration rose by about 18%.

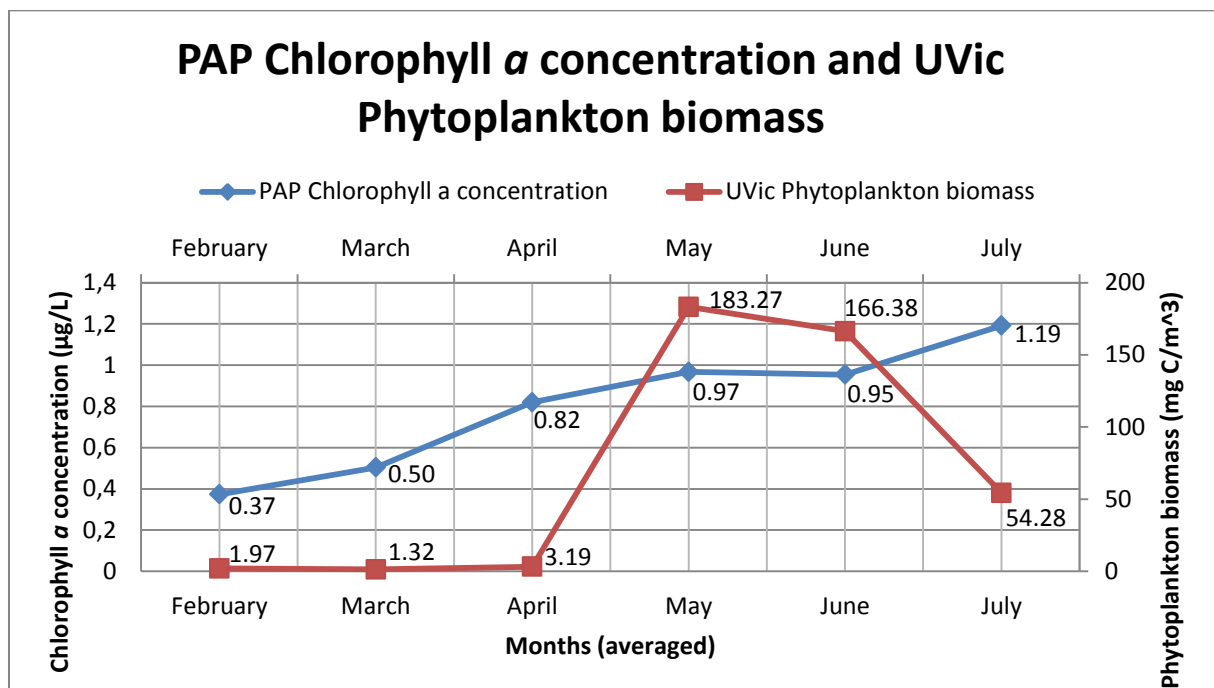


Figure 5: Chlorophyll *a* concentration (µg/L) measured by PAP Eurosite (blue diamonds) and UVic ocean phytoplankton biomass (mg C/m³) simulation (red squares) over time (months), at 49°N 16°W in the North Atlantic averaged over the years 2003-2012.

#### **4.2.2. Comparison of MODIS Chlorophyll *a* and UVic Phytoplankton biomass**

Regarding the analyzed region of the North Atlantic (30°-70°N 60°-10°W) the chlorophyll *a* concentration, observed by MODIS, increased slightly in the south developing northwards in February, with higher values north of 50°N (Fig. 6). In general they remained low, however, between 0 and 1 mg/m<sup>3</sup>. The model simulated low phytoplankton biomass values everywhere, except in the region 40°-60°N and 60°-40°W. A higher concentration of chlorophyll *a* at this region was not detected in the MODIS satellite image.

The chlorophyll *a* concentration remained low in March according to the MODIS satellite image, but an increase south of St. John's, Canada was visible (Fig. 6). At the same location the UVic phytoplankton biomass raised in March. In contrast to the MODIS data the highest phytoplankton biomass was predicted south of Greenland at 60°N.

The observed chlorophyll *a* content increased in April in the whole study area, especially near the coastlines and broadens further east (Fig. 6), while the UVic model simulated only a minor rise of phytoplankton biomass between Greenland and Canada as well as south of St. John's.

The MODIS data displayed great chlorophyll *a* concentrations from April on continuing until May, especially at 60°N around the Greenland coastline (Fig. 6). The UVic model simulated high phytoplankton biomass in the region between Canada and Greenland during April, which had a slightly different distribution in May. Additionally, high chlorophyll *a* values west of Canada at 50°N was shown by the satellite data in May, whereas the UVic model simulated high values of phytoplankton east and west of Greenland at 60°N and in the area around 50°N 15°W.

A clear decrease in chlorophyll *a* concentration over the whole study region was detected by the MODIS satellite during June. On the contrary, the UVic model simulated further increasing values of phytoplankton biomass north of 50°N (Fig. 6).

Further decline in chlorophyll *a* concentration was observed by the satellite in July. At that time also the UVic model forecasted lower values of phytoplankton, but with a great mismatch southeast of Iceland, caused by still rising phytoplankton biomass (Fig. 6).



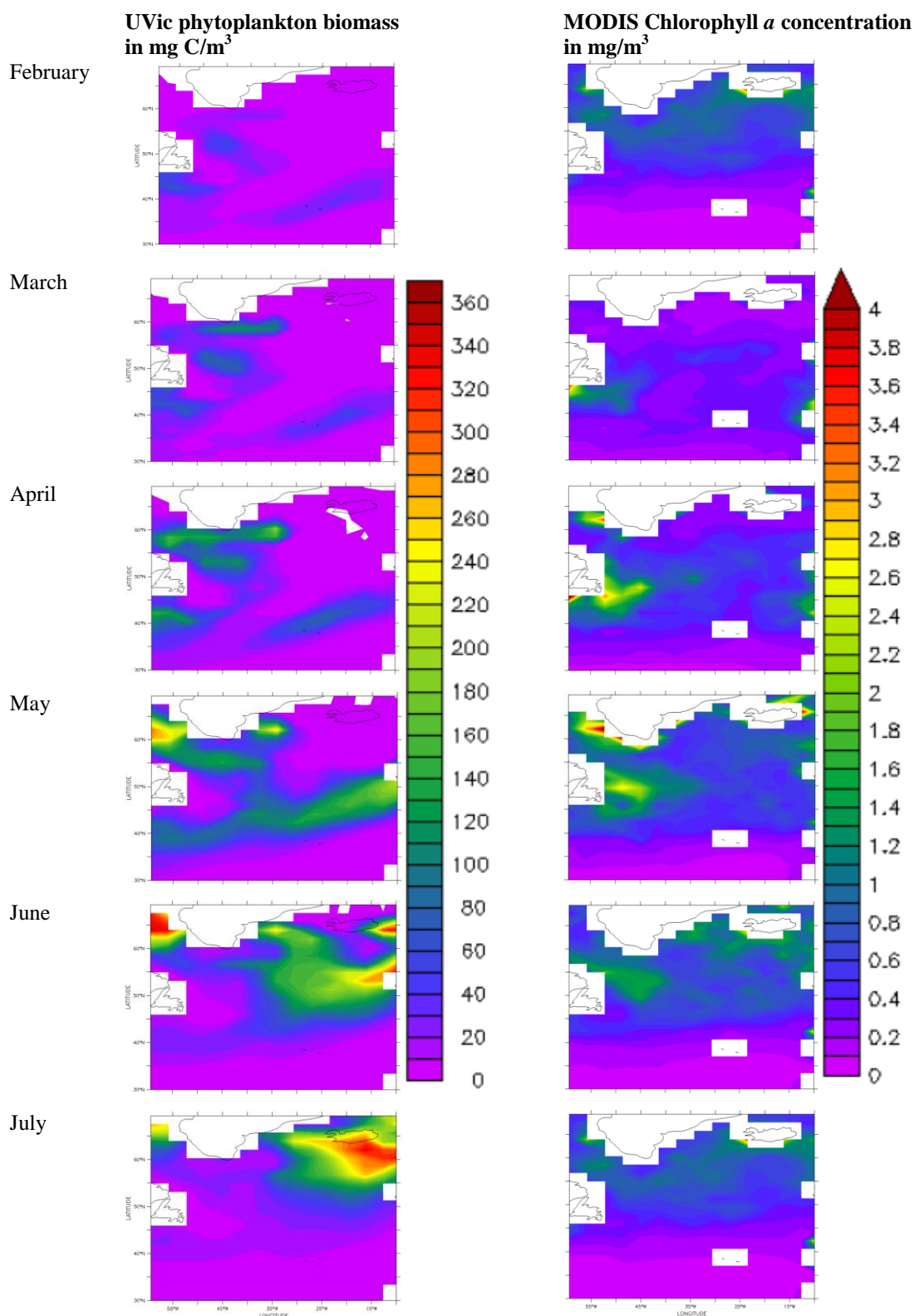


Figure 6: UVic phytoplankton biomass (mg C/m<sup>3</sup>) and MODIS chlorophyll *a* concentration (mg/m<sup>3</sup>) from February till July in the North Atlantic (30°–70°N 60°–10°W)

#### 4.2.3. Comparison of PAP and UVic Ocean Temperature

The simulated ocean potential temperature from the UVic model is generally lower than the CTD measured sea temperature at the PAP station (Fig. 7).

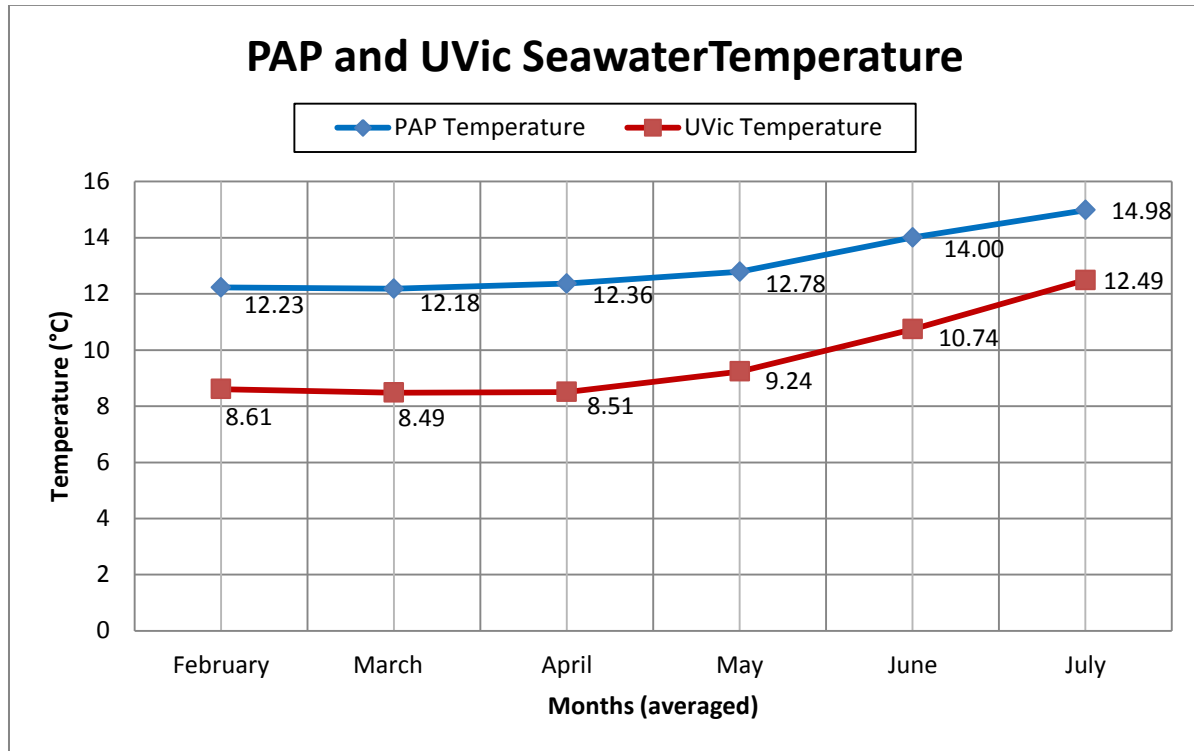


Figure 7: Seawater temperature measured by PAP Eurosite (blue diamonds) and UVic ocean temperature prediction (red squares) in °Celsius versus time (months), at 49°N 16°W averaged over the years 2003-2012.

To quantify these differences and to expose a more comprehensive evaluation, metrics, as defined by Stow et al. (2003, 2009), were calculated (Tab. 1).

**Table 1: Quantitative metrics for model skill assessment of seasonal results at 49°N 16°W**

Quantitative metric	Abbreviation	Temperature	Salinity
Root mean squared error	<i>RMSE</i>	3.44	0.28
Reliability index	<i>RI</i>	1.19	1.03
Average error	<i>AE</i>	-3.41	-0.28
Average absolute error	<i>AAE</i>	3.41	0.28
Modeling efficiency	<i>MEF</i>	-9.77	-577.62
Correlation coefficient	<i>R</i>	1.00	0.37

As seen in the temperature profile (Fig. 7) and also indicated by the correlation coefficient  $r$  (Tab. 1), the model prediction about observed temperature changes over time was significant ( $r=1$ ). In both cases the seawater temperature slowly increased from April on. To determine the multiplicative factor by which observed and predicted values differ, the reliability index  $RI$  (Leggett and Williams, 1981) was calculated and showed a value of 1.19. The  $RMSE$ ,  $AE$  and  $AAE$  had values around  $\sim 3.4$ , concerning the comparison of observed and simulated temperature. They measure the size of discrepancy between observed and expected values. Values near zero indicate a close match. The modeling efficiency  $MEF$  (Nash and Sutcliffe, 1970; Loague and Green, 1991) was calculated to discover the accuracy of model simulations to display observations. This value was less than zero ( $MEF=-9.77$ ), therefore the observation mean would predict the actual data better than the model simulation.

#### **4.2.4. Comparison of WOA09 and UVic Ocean Temperature**

The temperature values of WOA09 data and UVic simulation output, considering the whole study region, showed similar patterns in February (Fig. 8). The misfit between both illustrates, that the observed ocean temperature differed for about  $1-3^{\circ}\text{C}$  in the open ocean, while the difference at the east coast of Greenland and Canada were up to  $7^{\circ}\text{C}$ .

The same pattern was visible for March (Fig. 8). The temperature rose from February to March along the latitude gradient from south to north, causing a zonal temperature increase. The misfit slightly grew.

In April the misfit between the observed WOA09 data and the simulated temperature decreased in the open ocean slowly with the UVic model data generally underestimating the temperature of the measured data (Fig. 8).

This misfit grew because the temperature rise in the observed data happened much more rapidly than predicted by the model. The underestimation of temperature by the UVic model decreased further, as seen in data for May, and increased in June and July. The observed temperature zones reached further north and developed faster than simulated by the UVic model.

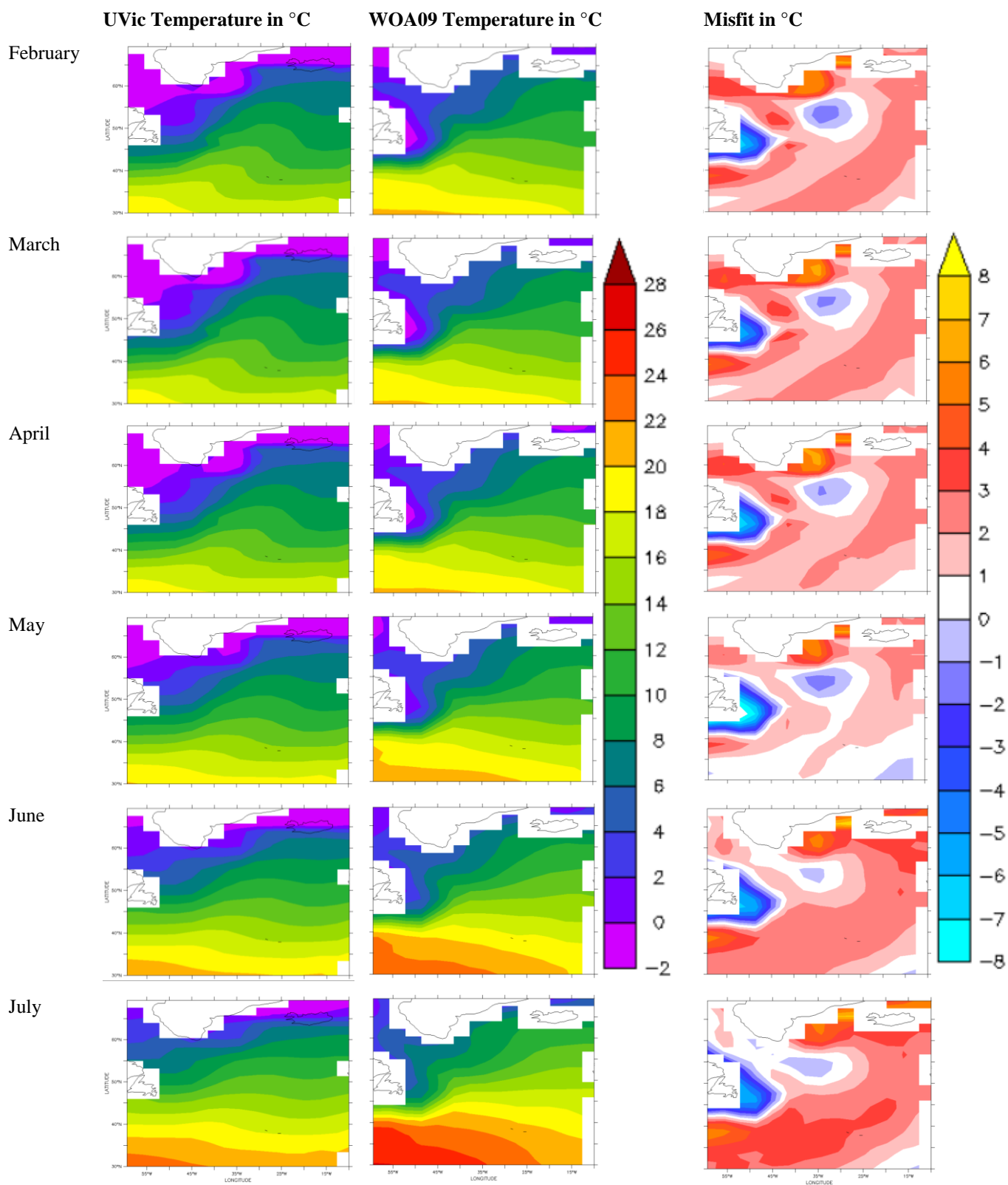


Figure 8: UVic ocean temperature (°C) and WOA09 ocean temperature (°C) from February till July in the North Atlantic (30°-70°N 60°-10°W).

#### 4.2.5. Comparison of PAP and UVic Ocean Salinity

The model derived sea water salinity varied on a scale of  $\sim 0.16 - 0.3$  PSU over the months compared with the salinity measurements at the PAP station (Fig. 9).

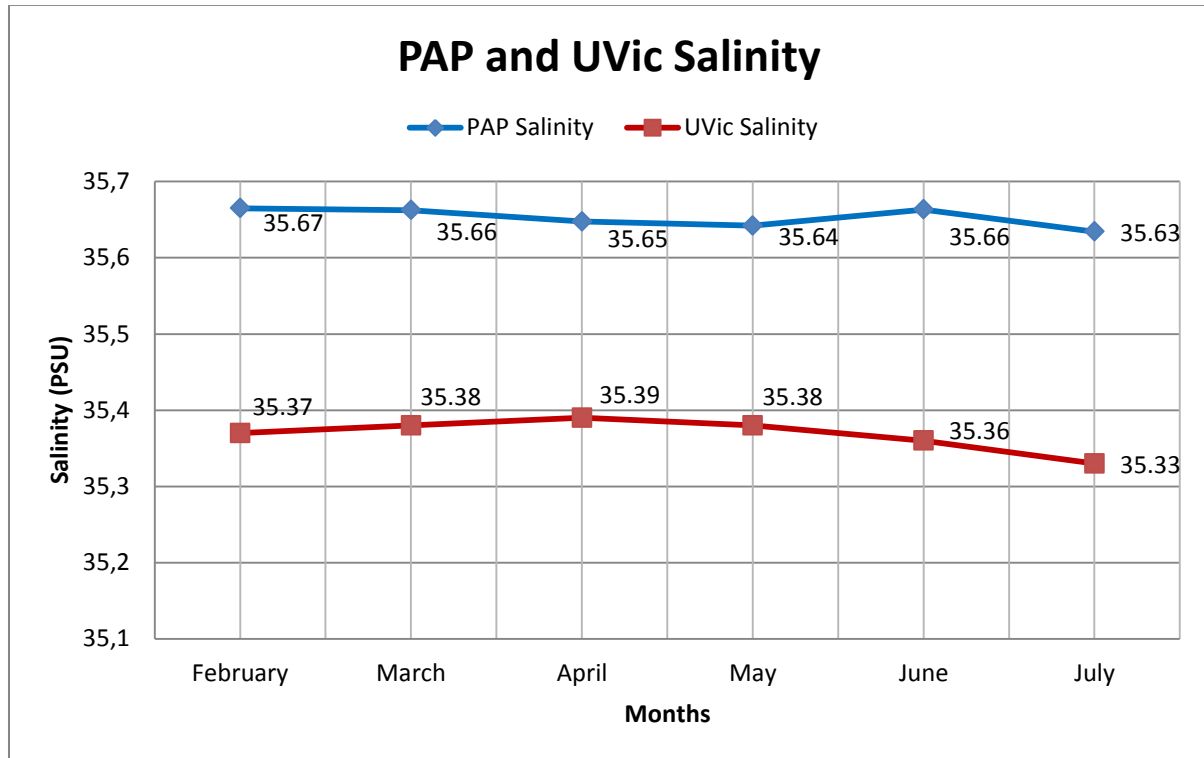


Figure 9: Seawater salinity measured by PAP Eurosite (blue diamonds) and UVic ocean salinity simulation (red squares) versus time (months), at 49°N 16°W.

But also here the model generally underestimated the measured values. The calculated metrics showed a close match between observations and simulations ( $RI$  near 1;  $RMSE$ ,  $AE$ ,  $AAE$  near 0; Tab. 1). The correlation coefficient is rather low ( $r = 0.3$ ), because the variation of the detected and predicted data over time showed a different pattern. The mean of observed data would predict values better than the UVic simulation, since the modeling efficiency was extremely high ( $MEF = -577.62$ ).

#### **4.2.6. Comparison of IFREMER and UVic Mixed layer depth**

By comparing simulations about the mixed layer depth in the North Atlantic study region with IFREMER observations a general shallowing of the mixing depth, starting in spring, was detected (Fig. 10). The observed data showed deep vertical mixing in February and March, in particular between Greenland and Canada as well as south of Iceland. East of St. John's was the only region where mixing depth shallower than 50m have been noticed (Fig. 10). A similar pattern was simulated by the UVic model. In April a slight decrease in the depth of the mixed layer in the southern part of the study region was measured and also predicted by the UVic model, although the observed shallowing of the mixed layer happened a lot faster than in the simulation. During May, June and July a shallow mixed layer depth was observed and also simulated by the model (Fig. 10), although the extent of the depth differed as IFREMER mixed layer depth was shallower than predicted. The UVic simulation also displayed deep mixing south of Iceland until June, while no deep mixing from May on had been observed.

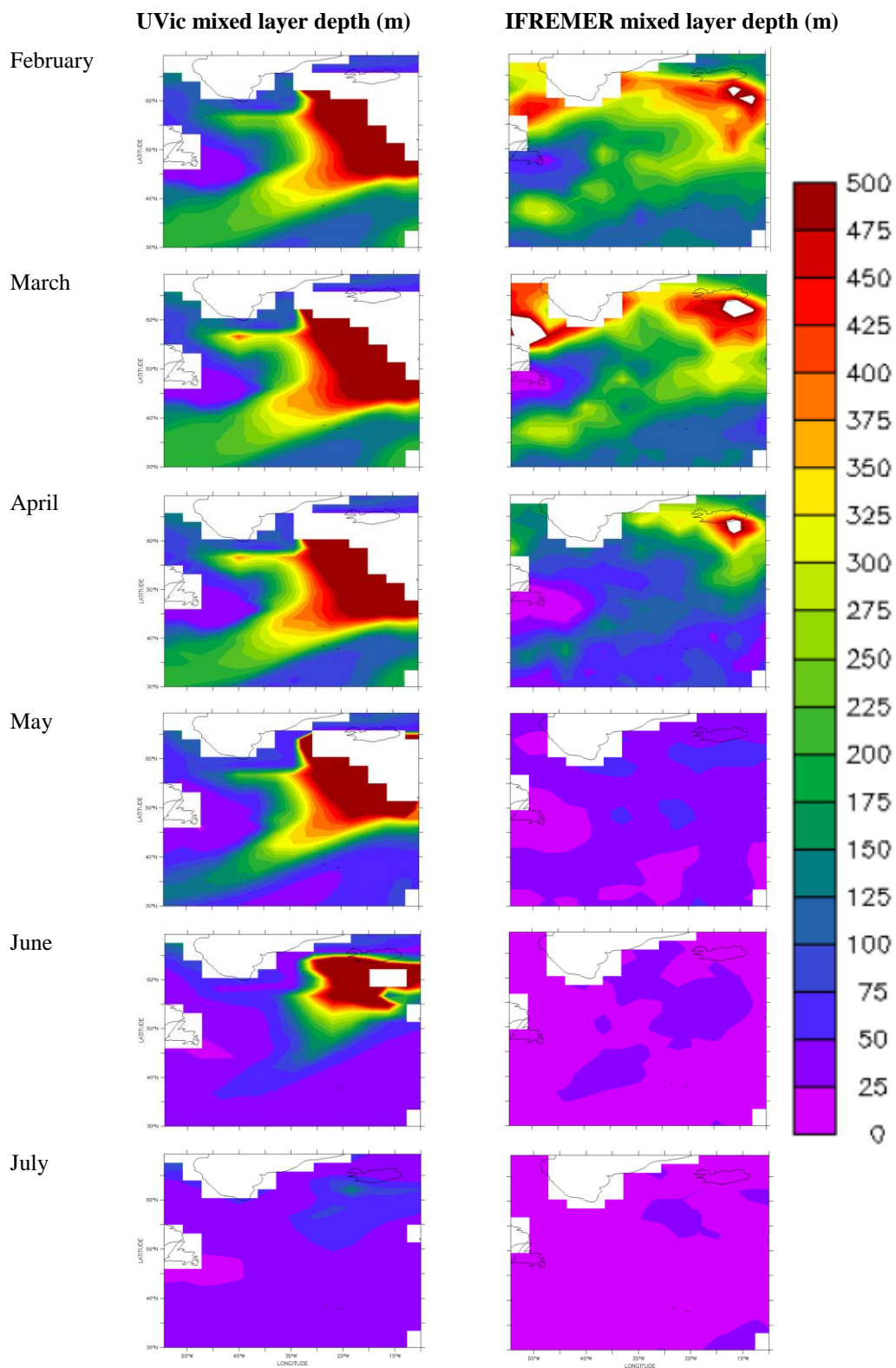


Figure 10: UVic mixed layer depth (m) and IFREMER mixed layer depth (m) from February till July in the North Atlantic (30°-70°N 60°-10°W).

### 4.3. Analyzing potential initiators of the simulated spring bloom

To investigate the triggering factors of the North Atlantic spring bloom in the UVic model correlations between the phytoplankton biomass and several parameters have been analyzed in this section.

#### 4.3.1. UVic Correlation of Phytoplankton and Ocean temperature

In the UVic model ocean temperature showed a high correlation with phytoplankton biomass in a broad area around Iceland in February, whereas south of Canada temperature and phytoplankton biomass seemed to correlate inversely (Fig. 11).

In March correlation of phytoplankton and temperature could only be observed in patches, but in April and May great areas in the study location showed a positive correlation between phytoplankton biomass and ocean temperature simulated by the UVic model. In June and July both parameters are significantly negative correlated for the most parts of the studied region.

At the PAP site (49°N 16°W) no significant correlation between phytoplankton biomass and ocean temperature could be detected (Tab. 2).

**Table 2: Correlation of Phytoplankton biomass and Ocean temperature at 49°N 16°W simulated by the UVic model**

	Correlation coefficient $r$ mean value (unweighted average)	Standard deviation $\sigma$
<b>February</b>	0.09	0.94
<b>March</b>	-0.42	0.82
<b>April</b>	0.11	1.00
<b>May</b>	-0.17	0.93
<b>June</b>	-0.37	0.94
<b>July</b>	-0.39	0.83



#### 4.3.2. UVic Correlation of Phytoplankton and the Mixed layer depth

The mixed layer depth, as simulated by the UVic model, was significantly correlated with the phytoplankton biomass in the western part of the studied area during February, while in the eastern part a negative relationship was visible (Fig. 11). In March the correlation of both parameters had a patchy distribution and became negative during April in most parts. Positive correlations of mixed layer depth and phytoplankton biomass have been simulated in the western part during May, developing further northwards during June and July.

Phytoplankton biomass and the mixed layer depth did not correlate significantly at 49°N 16°W in the UVic simulation (Tab. 3).

*Table 3: Correlation of phytoplankton biomass and Mixed layer depth at 49°N 16°W simulated by the UVic model*

	Correlation coefficient $r$ mean value (unweighted average)	Standard deviation $\sigma$
<b>February</b>	0.03	0.97
<b>March</b>	0.74	0.53
<b>April</b>	-0.32	0.85
<b>May</b>	0.19	0.88
<b>June</b>	0.68	0.68
<b>July</b>	0.45	0.84

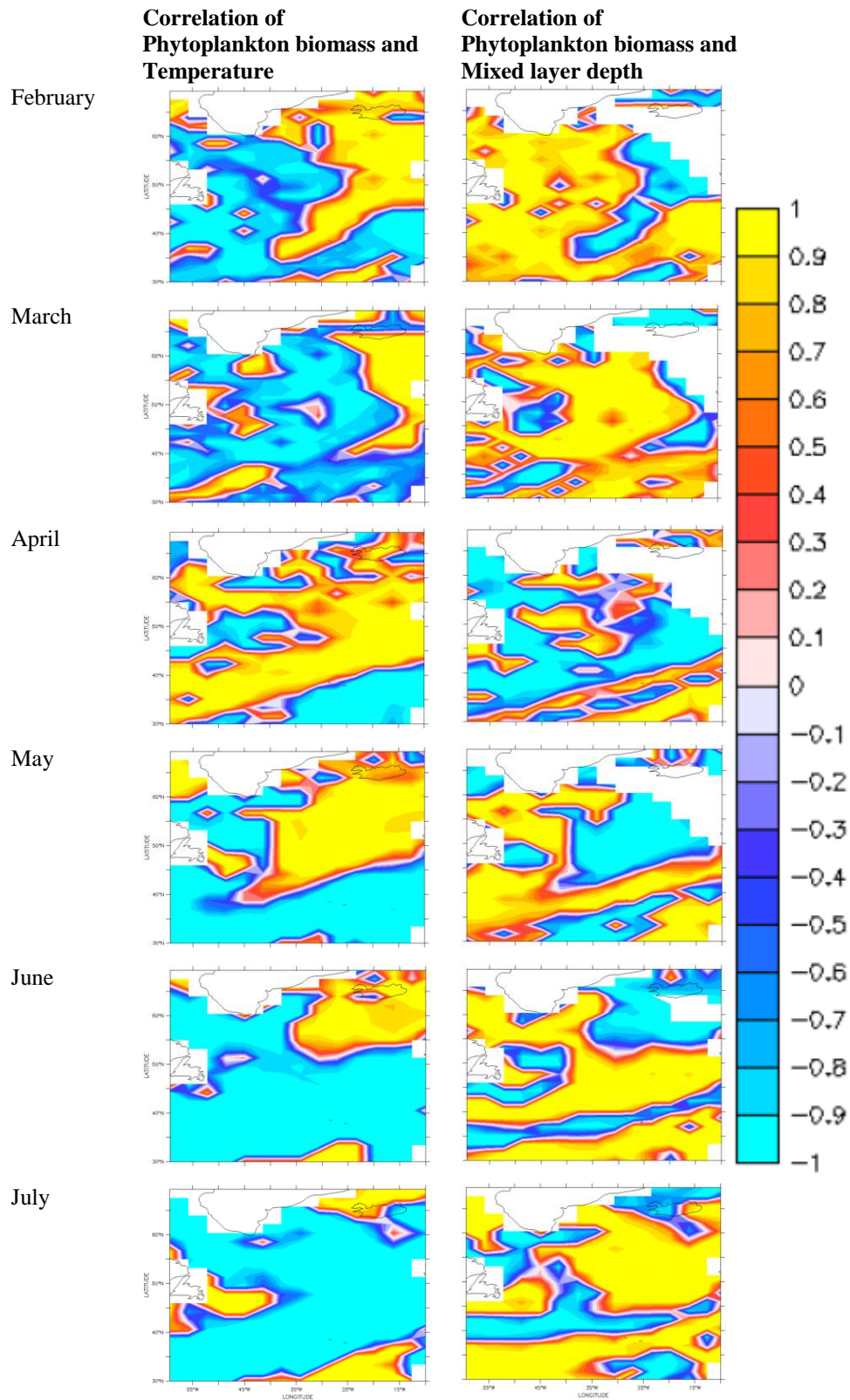


Figure 11: Correlation of UVic phytoplankton biomass with UVic ocean temperature and UVic mixed layer depth from February till July in the North Atlantic (30°-70°N 60°-10°W).

#### 4.3.3. Phytoplankton growth limitations by the UVic model

In this section phytoplankton growth limitations, in terms of solar radiation and nutrients, in the UVic model were analyzed (Fig. 12). In February most of the studied region was limited by irradiance, except for regions southward of 35°/40°N and eastward of St. John's, Canada, where nitrate was the limiting factor. The situation in March appeared similar, with a small additional nitrate-limited area south of Greenland. In April all stated nitrate-limited areas were enlarged. During May a huge part of the study region was limited by nitrate. The only light-limited region was northeast in the study region (45°-70°N 10°-35°W). This area shrank during June and in July, only the southern part of Iceland was still light-limited. The major part of the study area was at this time limited by nitrate. Phosphate never became the limiting factor in the study area.

#### 4.3.4. UVic Correlation of Phytoplankton and Nutrient content

During the first months of the modeling period phytoplankton biomass and nitrogen concentration showed a patchy correlation in the examined region (Fig. 12). Only from June on a significant positive correlation was found over a huge part of the region. The correlation of PO<sub>4</sub> concentration to phytoplankton biomass viewed similar (Fig. 13).

At 49°N 16°W no correlation between phytoplankton biomass and nitrate concentration could be found (Tab. 4).

**Table 4: Correlation of Phytoplankton biomass and Nitrate concentration at 49°N 16°W simulated by the UVic model**

	Correlation coefficient $r$ mean value (unweighted average)	Standard deviation $\sigma$
<b>February</b>	-0.64	0.70
<b>March</b>	-0.27	0.96
<b>April</b>	-0.17	0.78
<b>May</b>	-0.53	0.75
<b>June</b>	-0.55	0.82
<b>July</b>	-0.79	0.34

#### 4.3.5. UVic Correlation of Phytoplankton and Zooplankton biomass and grazing rate

Zooplankton biomass and phytoplankton biomass were highly correlated in most of the studied area over all examined months (Fig. 13). Only in March a negligible negative correlation was visible in small patchy parts of the North Atlantic region.

The grazing pressure on phytoplankton was highly correlated with the biomass of phytoplankton during all months in the examined region. Only negligible small patches showed other patterns. The only exception found, was in July, where an approximately 10 nm in diameter big patch southeast of Iceland displayed no significant correlation between grazing pressure and the content of phytoplankton.

Phytoplankton biomass and zooplankton biomass did not display any significant correlation at 49°N 16°W over the study period (Tab. 5). In contrast phytoplankton biomass and the grazing pressure on phytoplankton showed a significant positive correlation in February, April, June and July (Tab. 5). In March no correlation between both parameters were detected.

*Table 5: Correlation of Phytoplankton biomass and Zooplankton biomass and Grazing pressure on Phytoplankton at 49°N 16°W simulated by the UVic model*

	Correlation coefficient $r$		Standard deviation $\sigma$	
	mean value (unweighted average)			
	Zooplankton	Grazing pressure	Zooplankton	Grazing pressure
February	0.28	1.00	0.93	0.00
March	-0.49	0.04	0.84	0.73
April	0.43	0.98	0.77	0.05
May	0.29	0.90	0.80	0.13
June	-0.53	0.98	0.83	0.01
July	-0.23	0.99	0.89	0.02

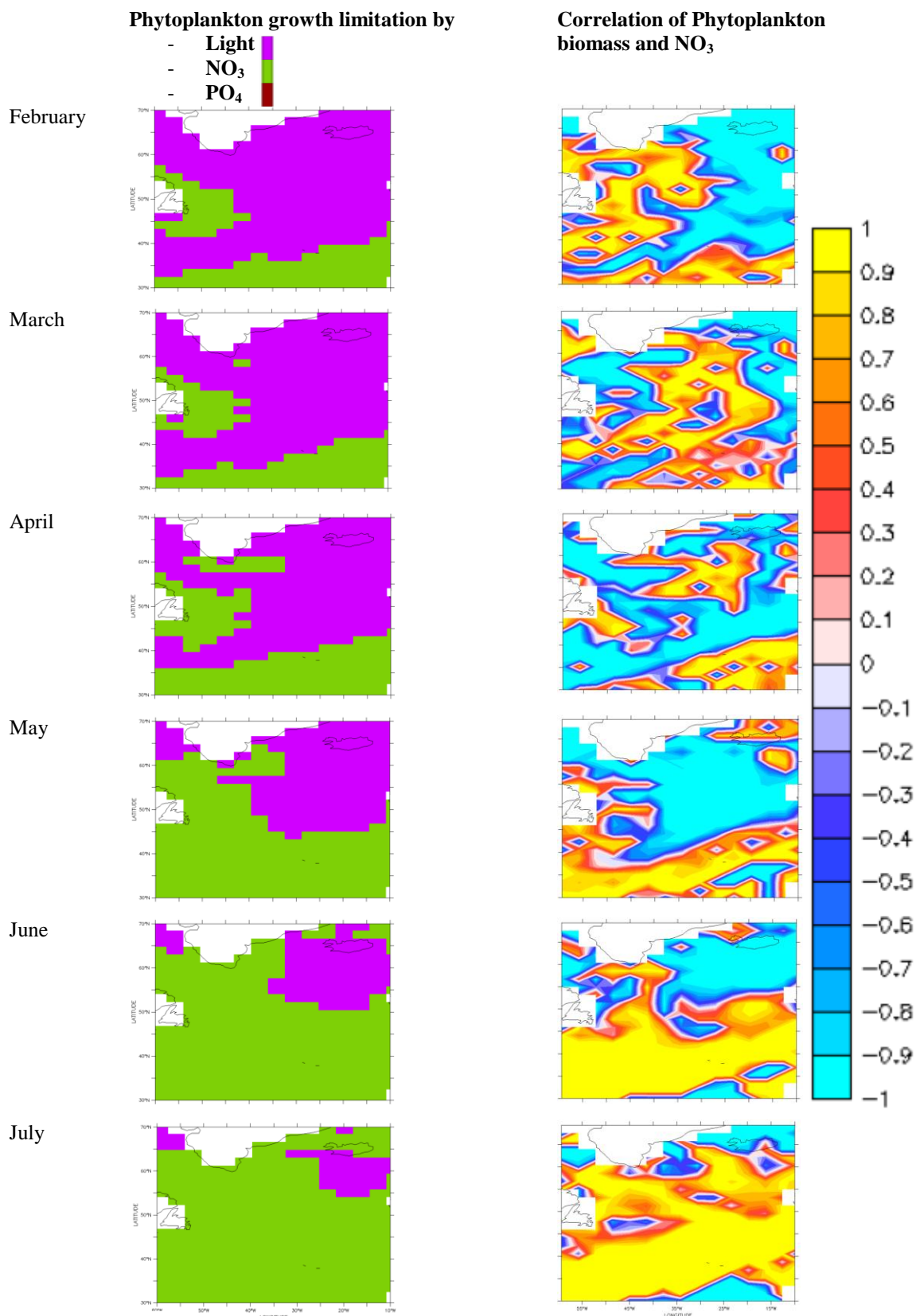


Figure 12: Limiting factors in UVic simulations on phytoplankton growth and correlation of UVic phytoplankton biomass with UVic nutrient concentration from February till July in the North Atlantic (30°-70°N 60°-10°W).

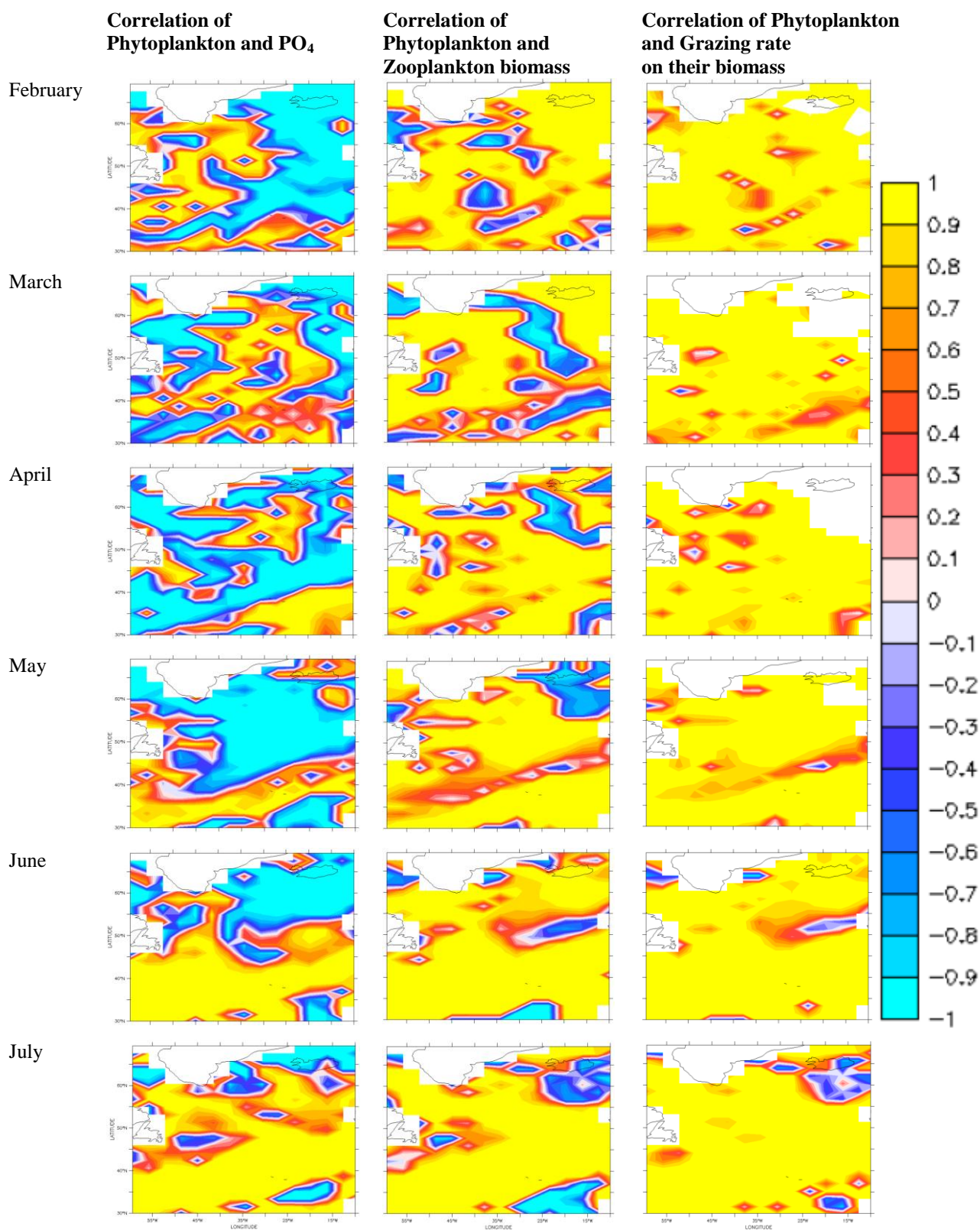


Figure 13: Correlation of UVic phytoplankton biomass with UVic PO<sub>4</sub> concentration, UVic zooplankton biomass and UVic grazing pressure on phytoplankton from February till July in the North Atlantic (30°-70°N 60°-10°W).



## 5. Discussion

Model simulations about Earth's climate system are a relevant tool to explore mechanisms and processes of biogeochemical cycling on a global and local scale and to investigate future changes in climate, especially those induced by anthropogenic activities.

To analyze the accuracy of model simulations, forcing factors and limitations (e.g. mixed layer depth, temperature, irradiance, nutrients, zooplankton grazing pressure) to the North Atlantic spring bloom, as predicted by the UVic model, were evaluated in this study.

### 5.1. Spring bloom timing and development

A clear discrepancy between observations and predictions has been detected by comparing the simulated phytoplankton biomass of UVic with observed chlorophyll *a* concentrations. Analyses at the PAP site and from MODIS satellite data demonstrated that the North Atlantic spring bloom initiation occurred in the beginning of April, approximately one month earlier (35-45 days) than simulated by the UVic model, as well as the bloom peak (25 days).

Not only the timing, but also the pace of bloom development was predicted inaccurately by UVic. While the measured chlorophyll *a* concentration increased on average of about 18% from April to May at 49°N 16°W, the UVic model simulated an immensely higher increase of about 5643% for the same timeframe. Observed blooms displayed for single years showed a steep increase at a specific time, nonetheless not as sharp as in UVic simulations. Furthermore the observed bloom was much patchier in the whole study region than simulated by UVic.

Additionally the observed high values of chlorophyll *a* concentration persisted longer at the PAP station than in the simulation, where a rapid decrease was detectable shortly after the blooms' peak. Further north UVic simulated a bloom in summer which had not been noticed by the MODIS satellite data.

In observations of previous studies, the North Atlantic chlorophyll *a* concentration in the middle of May was seven times higher than ~23 days before in the end of April (Bagniewski et al., 2011). A rough trend in the bloom development is the occurrence of highest chlorophyll *a* concentrations two weeks later for each 5° northward (Siegel et al., 2002a; Henson et al., 2008; Behrenfeld, 2010).

## 5.2. Ocean temperature

Both, observations and UVic predictions, showed an increase in temperature from May on. Simulations about monthly changes in temperature were significantly correlated to the measured seawater temperature. But the UVic model consistently underestimated the detected temperature in most parts of the study region, at the PAP site by 3,41°C, proved by the calculated *RMSE*, *AE* and *AAE*. The *MEF* revealed that the observation mean would better predict the actual ocean temperature than the UVic simulation.

The high correlation of phytoplankton biomass and temperature in some parts of the North Atlantic region, often near the coast, resulted from the temperature dependent growth formulation of simulated phytoplankton populations. Negative correlations in June and July could be attributed to decreasing phytoplankton biomass while temperature was still increasing.

At the PAP site no correlation between simulated phytoplankton biomass and simulated ocean temperature had been detected. This leads to the assumption that other factors than the warming of the upper water layer were controlling the phytoplankton bloom at this specific site.

The results are reconfirmed by previous observations as a temperature increase of the upper water layer had been observed during mid-May at the NABE site (47°N 20°W) (Lochte et al., 1993). The initiation of a bloom, which developed due to the warming of the upper water column, depends on the timing of a positive air-sea heat flux (Mahadevan et al., 2012). The heat loss of the North Atlantic at 40°N 40°W is usually due to long-wave reflection and evaporation. These processes are mainly influenced by cloud cover and wind stress. Short-wave radiation from the sun is the main heat source (Mann and Lazier, 2006).

But also phytoplankton blooms themselves can influence the North Atlantic water temperature by warming the surface layer of about 0.2°C, thereby causing a stabilization of the thermocline and further shallowing of the mixed layer depth (Mann and Lazier, 2006). This process is not parameterized in the model and thereby is not taken into account in the bloom simulation.



### 5.3. Mixed layer depth

Another crucial factor to the development of phytoplankton blooms is the depth of the mixed layer. Starting in April and strengthening during May, the mixed layer shallowed in observations and one month later in UVic simulations. This pattern had been detected also by previous examinations (Lochte et al., 1993; Bagniewski et al., 2011; Mahadevan et al., 2012). In NABE 1998 at the study site 47°N 20°W, and thereby close to the here studied location at 49°N 16°W, the mixed layer shoaled to a depth of 20-30m from previously >100m in late April, like in this examination, and decreased further by 10-20m in May (Lochte et al., 1993). This process caused an increase of phytoplankton biomass and thereby initiated the spring bloom (Lochte et al., 1993).

The UVic model simulated the shallowing of the mixed layer more uniform, but observations showed that the mixed layer depth shoaled inconsistently with heterogeneously distributed deep patches in the study region. These inaccurate estimations of the UVic model concerning the mixed layer depth can have an influence on the accuracy of the simulated spring bloom.

The salinity values, which are related to the mixed layer depth, showed a close match between observations and simulations, since *RMSE*, *AE* and *AAE* were near 0. But *MEF* and *r* revealed an inaccurate simulation of salinity changes over time.

Phytoplankton biomass and the mixed layer depth showed a positive correlation over major parts of the study area, except some patches and bands, which displayed opposite relations. Noticeable is, that April was the only month where a clear negative correlation between both variables in nearly the whole region was visible. In April the mixed layer was still deep. Phytoplankton biomass levels in contrary started to increase, so the magnitude still remained low. Shallow mixing depths can promote phytoplankton populations growth. The correlation analysis at the location 49°N 16°W showed no significant correlation during the study period.

#### **5.4. Light and nutrient limitations to the spring bloom**

By analyzing the controlling factors on phytoplankton growth, a general northward trend of nitrate limitation substituting the previously predominating light limitation was detected. The correlation of nitrate and phosphate to phytoplankton biomass was patchy in the first months and results then in a high correlation during summer in huge parts of the study area. Decreasing phytoplankton biomass in the southern regions was associated with declining nitrate concentrations there. Also at the PAP station site a contrary trend of phytoplankton biomass and nutrients had been detected, although no significant correlation can be named.

Nitrate and phosphate are important nutrients for phytoplankton, their growth, reproduction and productivity. Due to the thermocline, vertical mixing is diminished and virtually no new nutrients are entrained from below. Consequently nutrients, in particular nitrate, are depleted by phytoplankton consumption during periods of a stratified water column.

Irradiance is steadily increasing in the North Atlantic from spring on. But the UVic model simulation of irradiance takes diurnal cycles and cloud cover not into account. Furthermore the role of light as a limiting factor is questionable, because Marshall and Orr (1928) discovered that also in winter enough solar radiation is accessible for phytoplankton to increase their biomass in particular subpolar regions.

Because phosphate did not play a limiting role for algae growth in the region of interest, according to the UVic simulation, and correlations with phytoplankton have the same distribution like nitrate, phosphate is not further considered in this study.

#### **5.5. Zooplankton biomass and grazing rates**

Spring blooms are also affected by the grazing pressure of heterotrophs. Since phytoplankton biomass was already increasing while zooplankton biomass remained low in some areas, the correlation of both parameters was relatively patchy until May. In June and July most of the study region showed a positive correlation between both parameters in MODIS satellite images. In contrast no clear trend was visible at the PAP station.

Zooplankton growth is dependent on the species and their adaptation to temperature changes. The UVic version used here allowed the growth rate to change with temperature (Keller et al., 2012). Therefore the population may still have negative growth rates in early spring due to the

cold environment. Their phenological cycles are significantly dependent on phytoplankton, as they present a main source of zooplankton diet, depending on the species (Calbet and Landry, 2004; Keller et al., 2012).

As phytoplankton biomass was estimated considerably wrong by the UVic model also zooplankton biomass simulations could be wrong and further investigation is necessary to discover the ability of the UVic model to simulate zooplankton population dynamics. Diel vertical migration may additionally cause inaccurate estimates of zooplankton biomass in general.

Phytoplankton biomass and the grazing rate on them are significantly correlated, except in March, where no clear relationship of both parameters was shown. The grazing rate is a main regulatory process of phytoplankton abundances during summer in the North Atlantic (Behrenfeld, 2010), but the magnitude of its impact is still under debate, because estimates are mostly based on improper *in situ* studies without regard to water column turbulences (Mann and Lazier, 2006).

## **5.6. Other potential factors and influences**

The here demonstrated irregular distribution of phytoplankton spring blooms was observed previously. Phytoplankton primary production is not homogeneously distributed, but patchy in space with temporary peaks over several weeks as revealed by satellite data (Dutkiewicz et al., 2001; Taylor and Ferrari, 2011; Signorini et al., 2012). Lochte et al. (1993) already postulated a spring bloom to be “a patchwork developing northwards”, which applies also for the North Atlantic region (Watson et al., 1991; Mahadevan et al., 2012).

This can be caused by different environmental events or conditions, like internal waves, mesoscale fronts or eddies (Fasham, 1976; Mann and Lazier, 2006), and is related to the stratified conditions of the water column, as both, observational studies and model simulations, showed (Mann and Lazier, 2006; Mahadevan et al., 2012). Small and mesoscale eddies with an extent of <100km have been detected in the Northeast Atlantic regularly in former studies (Krauss et al., 1990; Lochte et al., 1993). In the North Atlantic eddies are significantly correlated with patchy phytoplankton assemblages and stratified areas with high primary production (Savidge et al., 1992; Townsend et al., 1994). The UVic model cannot

simulate these physical features and does not include brief transient drivers, which could be one reason for the incorrect simulated timing.

Also meteorological circumstances during the development of a bloom are pivotal if the water column is subject to a transient stratification (Stramska et al., 1995; Waniek, 2003). When warming winds and storms occur, the phytoplankton biomass and production rates are suppressed although nutrients are re-introduced to the surface layer.

Areas with a positive correlation between phytoplankton biomass and ocean temperature often existed near the coast. A factor causing elevated phytoplankton values could be the input of trace elements and the freshwater runoff from land (Mann and Lazier, 2006), since introduced low salinity waters stabilize the water column. This is supported by IFREMER observed mixed layer depth values. Examining this object will provide further understanding of environmental conditions triggering a phytoplankton bloom.

### **5.7. Spring bloom formation**

The formation of a bloom happens differently depending on the forcing processes. A patchier distribution is expected by blooms evolved from eddy restratification, in contrast to blooms formed by the warming of the upper water layer (Mahadevan et al., 2012). The latter process is more homogenous, since it acts over a larger scale, while eddies are a local event.

This examination showed that the observed bloom developed patchier than the simulated UVic bloom, which leads to the assumption that different driving factors act on the simulated blooms than actual in the ocean. In observations mixing depths were already shallowing, while temperature started to raise in May according to both, WOA09 and IFREMER data. Hence blooms occurring in April are not caused by enhanced temperature in observations. The UVic model simulated temperature rise and mixed layer shoaling to happen both in May.

Noticeable is the higher phytoplankton biomass and chlorophyll *a* concentration at the southeast coast of St. John's, Canada, in this study. The mixed layer depth first and most shallowed at this location, in observations slightly more and considerably earlier than in the UVic simulation. The model overestimated the temperature around St. John's. It may be that the simulated spring bloom, displayed at this study site, is caused by the higher temperature

estimates, and not due to shallower mixing depths, as it is the case according to the satellite images.

The observations support the Critical-Depth-Theory by Sverdrup (1953), while the simulation did not follow this hypothesis, concerning the mixed layer depth. The water column stratification seems to play only a minor role in initiating the simulated bloom.

In this examination the simulated nitrate availability was limiting the bloom development in the UVic model throughout the summer. This result is consistent with assumptions made by the Critical-Depth-Theory (Sverdrup, 1953).

Another determining factor for the simulated bloom was the zooplankton grazing pressure. In the ocean eddies and turbulences, for example, can prevent the merging of phytoplankton and zooplankton populations. This can influence their growth rates and also the timing of bloom formation according to the Dilution-Recoupling-Hypothesis. But it is questionable if the model simulates this de- and recoupling according to Behrenfeld (2010) due to the actual factors, as deep mixing. It is more probable that simulated temperature differences cause the temporal decoupling of phytoplankton and zooplankton populations, because their growth is connected to temperature in the UVic model.

These findings state the importance of analyzing the contribution of the mixed layer depth and other related parameters to the initiation and timing of phytoplankton bloom development, as they affect population size and growth rates in spring.

## 6. Conclusion

### 6.1. Suggestions for modeling improvements

There has been a fast development of ecosystem models simulating physical, chemical and biological processes of the upper water column in the oceans (e.g., Oschlies and Garcon, 1998; Moore et al., 2004; Doney et al., 2009), investigating climate variability seasonally and interannually (e.g., McKinley et al., 2004; Le Quéré et al., 2007), with respect to future climate scenarios (e.g., Bopp et al., 2003).

Increasing complexity of ecosystem models may improve the correctness of their predictions in comparison with simpler models. But this also produces the need of taking more parameters into account, which are not well understood yet. The rising number of parameters makes optimization attempts more complex and problematic (Bagniewski et al., 2011).

Future climate change and interannual variability can influence vertical mixing events in the upper ocean water column during spring, whereas stratifying processes in coastal regions are controlled by tidal mixing (Pingree et al., 1976; Townsend, 1994). The stabilization of the water column is often induced by vertical forces in simulations, but horizontal gradients should also be better parameterized, due to their role in eddy stratification (Fox-Kemper et al., 2008; Mahadevan et al., 2012). Their contribution in the initiation of the spring bloom and the related phytoplankton primary production, requires the parameterization of lateral processes (Fox-Kemper et al., 2008; Taylor and Ferrari, 2011; Mahadevan et al., 2012).

This study showed that the North Atlantic spring bloom is initiated prior to the simulated UVic bloom. Previous studies already discovered that models often simulate the bloom start date and development later than the observed phytoplankton spring bloom in temperate regions (Townsend et al., 1994). The development of a bloom is governed by cloud cover, the associated solar radiation budget as well as atmosphere-ocean heat flux, the shallowing of the mixed layer and wind stress (Townsend et al., 1994). But the initiation of the North Atlantic spring bloom regulated by eddies is often undetected by existing ocean ecosystem models, and also in the UVic simulation, since the influence of eddy restratification on bloom formation has not been parameterized in the model. Further investigation is needed to analyze at which locations phytoplankton blooms are caused by eddies to improve model skills. Therefore analyses are necessary to discover how eddy induced blooms can be simulated by climate models.

Since wind stress is a major driver of the seasonal and interannual variability in water column stratification, with respect to mixed layer depth and phytoplankton blooms (Martinez et al., 2011), this variable should be the object of further studies. Additional attention should be drawn on the upwelling of nutrients and the influence of freshwater runoff and trace elements.

Models, predicting conditions and processes in the upper ocean precisely, may fail to simulate the environment of the deep ocean and associated export rates (Bagniewski et al., 2011). Due to the importance of biological export of carbon for future climate alterations, model simulations ability concerning the deep sea environment and the twilight zone should be improved (Bagniewski et al., 2011). Further investigations are needed to evaluate the ability of the UVic model to simulate these processes and the accuracy of CO<sub>2</sub> sequestration to the deep ocean.

Simulating the formation of diatom aggregates and their sinking velocity can be an important parameter to estimate the atmosphere-ocean carbon flux as well as the development and termination of spring blooms more accurately (Bagniewski et al., 2011). Also coccolithophores contribute substantially to the export of carbon (Signorini et al., 2012). To improve future simulations of the North Atlantic spring bloom and their contribution to carbon sequestration in general, future climate models should contain the main phytoplankton groups (Signorini et al., 2012). But since UVic is a model of intermediate complexity it is questionable if the rise in complexity is that essential and doable. Further analyzes are necessary to investigate if models including this parameterization will lead to significant better simulations about phytoplankton population development than the UVic model. Useful tools to optimize biogeochemical models are field observations of “high-resolution interdisciplinary data from autonomous platforms” (Bagniewski et al., 2011).

Oceanic conditions and processes are, despite plenty research effort, still uncertain. To develop adequate equipment to ascertain their values and variability is challenging (Waniek, 2003). Especially phytoplankton loss rates due to “grazing, respiration and remineralisation, are problematic to detect” (Waniek, 2003). Optimized ecosystem models are needed to better predict distributions of phytoplankton blooms and the related physiological, chemical, physical and biological circumstances initiating their development and causing their termination.

## **6.2. The impact of climate change**

The temperature of Earth's upper ocean layer has increased 0.5 to 0.7 degrees on average during the last century (IPCC, 2007). This warming affects marine ecosystems and their biogeochemical cycles as well as phytoplankton primary production (Taucher and Oschlies, 2011). The upper water column is assumed to stratify earlier and longer with further greenhouse warming (Sarmiento et al., 2004; Cole et al., 2012). On the one hand this will advance the solar radiation budget in the stratified water column at higher latitudes, leading to a longer growth period for light-limited phytoplankton populations (Bopp et al., 2001). On the other hand the nutrient content in the upper water layer is a limiting factor, particularly with elongated stratification. The thermocline acts as barrier, hindering the vertical re-supply of nutrients, which will diminish the bloom formation at mid and low latitudes (Behrenfeld et al., 2006; Cole et al., 2012). Thereby phytoplankton bloom dynamics in certain areas may be changed in terms of bloom start date, intensity and duration (Townsend et al., 1994).

This will also influence the trophic chain, since the seasonally-dependent timing of phenological cycles of phytoplankton and higher trophic levels control their survival and reproduction rates (Cushing, 1990; Platt et al., 2003; Cole et al., 2012).

Consequences for the trophic chain, including zooplankton, invertebrates and fish, could be that the pelagic community will benefit much more of increased production rates, linked to longer stratification periods, because of decreased export of organic material to the benthos (Frank et al., 1990; Townsend et al., 1994).

Following Sverdrup's theory, the North Atlantic bloom is expected to occur earlier in spring and have enhanced chlorophyll *a* concentrations. In contrast to the prior the Dilution-Recoupling Hypothesis of Behrenfeld (2010) claims that less deep mixing in winter will cause lower phytoplankton growth rates, which is supported by satellite data, displaying a negative correlation of chlorophyll *a* concentration to sea surface temperature in the subpolar region (Behrenfeld et al., 2008, 2009, 2010).

Since the simulated phytoplankton bloom may be controlled by temperature near St. John's in the UVic model and temperature is expected to increase, a more homogeneous bloom development could be formed. The predicted bloom start date will occur earlier, due to higher temperature estimates. Observations in contrast assume patchier blooms with higher regional heterogeneity caused by mixed layer eddies (Mahadevan et al., 2012).



Still uncertain are the possible influences of an anthropogenic altered climate system on the oceanic environment and the effects of recently postulated climate engineering technologies on the biological pump (Frank et al., 1990; Townsend et al., 1994; Keller et al., 2012).

### **6.3. The impact of methods and missing data**

To investigate the initiation, structure and development of the North Atlantic spring bloom and related parameters different techniques are available. Although they are useful tools their deficits should be taken into account.

According to Platt et al. (2010), the investigation of phytoplankton life cycles over a large study area during a long time period by remotely sensing of ocean color is a valuable tool, which is used in this study in form of MODIS images of chlorophyll *a* concentrations. Even though satellite data can only examine the ocean's surface and a small number of features, they have a high spatio-temporal resolution and are therefore able to discover short-lived blooms of phytoplankton (Doney et al., 2009; Mann and Lazier, 2006). Seasonal or interannual variations like this may remain undetected by ship-based investigations. The sampling by mooring stations and research cruises is necessary to identify the vertical alteration of biogeochemical features, but they are limited in number (Doney et al., 2009) and can only give a snap shot of certain phytoplankton bloom patches and their development (Bagdewski et al., 2011). This is the case for the PAP station data, where different parameters over different depths were examined, but at a fixed station.

When analyzing the importance of climate seasonality and phytoplankton blooms the impact of missing data has to be considered. Data gaps make approximations uncertain and the unnoticed of interannual and seasonal variations in phytoplankton blooms, their timing and duration trends is a challenging issue (Cole et al., 2012).

Especially at higher latitudes, like the North Atlantic region studied here, persistent cloud and ice cover, winter low sun angles and aerosols in the atmosphere, are problematic phenomena causing massive data gaps (Cole et al., 2012). Seasonal variability especially regular occurring events and their timing of initiation and collapse can be difficult to determine with missing data.

These factors could therefore affect the accuracy of observed data about phytoplankton bloom development and the bloom start date as well as other examined parameters in this study. Additionally the data were averaged over time. Although this method reduces the effect of missing data, it also “smoothes out high-frequency variability” (Winder and Cloern, 2010; Cole et al., 2012). Unnoticing of seasonal variations of parameters or extreme events can be the consequence. Therefore a penetrating analysis is necessary in further studies to investigate the influence of data gaps on phytoplankton bloom examinations.

Former studies found that regions highly affected by data gaps show timing errors up to 30 days to early for the bloom start date and vary around 15 days when predicting the bloom peak date. But predictions were also found to be wrong for up to 50-60 days in the spring bloom start date north of 40°N in the western part of the North Atlantic (Cole et al., 2012). In general averaging data with plenty gaps causes predicted bloom initiation dates to be later than in reality. This is typical at high latitudes, which are greatly affected (Dandonneau et al., 2004), although only minor cloud cover in summer is assumed to influence the data (Cole et al., 2012).

The study period to examine the phytoplankton spring bloom has been from February till July, but references exist that propose the onset of increased phytoplankton growth rates to be in winter and thus assuming a three to five fold greater biomass then so far suggested during this time period (Behrenfeld, 2010; Waniek, 2003). An extension of the study time period over the whole year could validate this hypothesis. On the other hand chlorophyll *a* concentrations estimated by satellite data seem to be lowest in January (Banse, 2002; Backhaus et al., 2003; Ward and Waniek, 2007; Behrenfeld, 2010).

Furthermore the UVic model does not differentiate between the first 50 meter of the ocean, so important and sensible processes and mechanisms related to specific mixing depths stay undetected. A more detailed separation of the upper water column is necessary to discover the bloom formation more precise.

Improving the quality of examination methods to optimize forecasts in these areas is pivotal, due to their high productivity rates and high variability in seasonal cycles (Cole et al., 2012).

## 7. Summary

It is of major importance to put more effort in examining simulated ecosystem seasonality because the changes in climate will have a major effect on the timing, intensity and duration of the phytoplankton spring bloom and these processes can lead to species shifts and alterations in biogeochemical cycles, which will not be detected on an annual scale.

This study showed, that the occurrence of the North Atlantic phytoplankton bloom is not predicted accurately enough by the UVic model for solid predictions about CO<sub>2</sub> sequestration, biological pump magnitude and other biological and physical interaction processes.

As shown before, the UVic model simulated the North Atlantic spring bloom approximately one month too late. Also the predicted phytoplankton population growth rates differ to observations. Temperature changes are correlated significantly, but the actual temperature has been underestimated by the model.

The model does not correctly predict the timing and causes of the North Atlantic spring bloom. Temperature, not mixed layer depth, most probably controlled the simulated bloom at a specific study site. At other locations of the study region no distinct driving factor could be identified. The shoaling of the mixed layer depth has to be better parameterized in the UVic model to achieve an optimized simulation and to discover the influence of this process to the phytoplankton bloom. While the UVic bloom in the North Atlantic was first limited by light, nutrient limitations were pivotal in summer. The UVic simulation showed a more uniform shallowing of the mixed layer depth than observed.

At summer time also zooplankton grazing may act as a main regulatory process terminating a phytoplankton bloom. But estimates about population size and dynamic of both, phytoplankton and zooplankton, is based on measurements that are too inaccurate for displaying population dynamics in marine ecosystems adequate, especially water column turbulences and eddies are not taken into account properly.

More effort has to be made to analyze causes and consequences of the North Atlantic spring bloom and more study effort for making UVic simulations more precise in simulating phytoplankton blooms is necessary. Since irradiance also have a huge impact on bloom development, also researches analyzing if irradiance measured by satellite data and simulated irradiances are correlated has to be done, but cloud cover and other factors causing data gaps,

should be taken into account properly. Also weather phenomena on a weekly base are highly influencing timing and duration of bloom patches, a closer look on this subject should be taken. Investigating the role and importance of wind velocities and eddies, as positions of local upwelling, on the phytoplankton growth formulation in earth system climate models seems to be a necessary project. Since UVic is a model of intermediate complexity, at least some of these topics have to be examined with other climate models.

To conclude: A lot more work has to be done to analyze and improve simulations of phytoplankton blooms in the North Atlantic by the UVic model. Although there are many influences that play a role in phytoplankton life cycles and bloom development, to keep the simulation feasible the suggestion is to correct predicted temperature values and to improve the simulations of the mixed layer depth and bloom development by taking eddies and wind stress more into account first of all, by better parameterizing these variables without adding too much additional complexity.

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## 9. References

- Atkins, W.R.G. (1928). Seasonal variation in the phosphate and silicate content of sea water during 1926 and 1927 in relation to the phytoplankton crop. *Journal of Marine Association* 15, pp. 191–205.
- Anderson, T.R. (2005). Plankton functional type modelling: running before we can walk? *Journal of Plankton Research* 27 (11), pp. 1073–1081.
- Backhaus, J., Wehde, H., Hegseth, E.N. and Kämpf, J. (1999). “Phytoconvection”—on the role of oceanic convection in primary production. *Marine Ecology Progress Series* 189, pp. 77–92.
- Backhaus, J.O., Hegseth, E., Wehde, H., Irigoien, X., Hatten, K. and Logemann, K. (2003). Convection and primary production in winter. *Marine Ecology Progress Series* 215, pp. 1–14.
- Bagniewski, W., Fennel, K., Perry, M.J. and D'Asaro, E.A. (2011). Optimizing models of the North Atlantic spring bloom using physical, chemical and bio-optical observations from a Lagrangian float. *Biogeosciences* 8 (5), pp. 1291–1307.
- Banse, K. (1992). Grazing, temporal changes of phytoplankton concentrations, and the microbial loop in the open sea. In *Primary Productivity and Biogeochemical Cycles in the Sea*, edited by Falkowski, P.G. and Woodhead, A.D., pp. 409–440, Plenum, New York.
- Banse, K. (2002). Steeman Nielsen and the zooplankton. *Hydrobiology* 480, pp. 15–28.
- Baudoux, A.-C., Noordeloos, A.A.M., Veldhuis, M.J.W. and Brussaard, C.P.D. (2006). Virally induced mortality of *Phaeocystis globosa* during two spring blooms in temperate coastal waters. *Aquatic Microbial Ecology* 44(3), pp. 207–217.

- Behrenfeld, M.J. and Boss, E. (2006). Beam attenuation and chlorophyll concentration as alternative optical indices of phytoplankton biomass. *Journal of Marine Research* 64, pp. 431–451.
- Behrenfeld, M.J., Siegel, D.A. and O'Malley, R.T. (2008). Global ocean phytoplankton and productivity. In: *State of the climate in 2007*, in Levy, J.M., editor. Bulletin of the American Meteorological Society, pp.56– 61.
- Behrenfeld, M.J., Siegel, D.A., O'Malley, R.T. and Maritorena, S. (2009). Global ocean phytoplankton. In: *State of the climate in 2008*, in Peterson, T.C. and Baringer, M.O., editors. Bulletin of the American Meteorological Society, pp. 568–573.
- Behrenfeld, M.J. (2010). Abandoning Sverdrup`s Critical Depth Hypothesis on phytoplankton blooms. *Ecology* 91 (4), pp. 977–989.
- Bopp, L., Monfray, P., Aumont, O., Dufresne, J.L., Le Treut, H., Madec, G., Terray, L. and Orr, J.C. (2001). Potential impact of climate change on marine export production. *Global Biogeochemical Cycles* 15(1), pp. 81–99.
- Bopp, L., Aumont, O., Belviso, S. and Monfray, P. (2003). Potential impact of climate change on marine dimethyl sulfide emissions. *Tellus B* 55, pp. 11–22.
- Brody, S.R., Lozier, M.S. and Dunne, J.P. (2013): A comparison of methods to determine phytoplankton bloom initiation. *Journal of Geophysical Research-Oceans* 118(5), pp. 2345–2357.
- Calbet, A. and Landry, M.R. (2004). Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnology and Oceanography* 49(1), pp. 51–57.
- Claussen, M., Mysak, L. A., Weaver, A. J., Crucifix, M., Fichefet, T., Loutre, M.-F., Weber, S. L., Alcamo, J., Alexeev, V. A., Berger, A., Calov, R., Ganopolski, A., Goosse, H., Lohmann, G., Lunkeit, F., Mokhov, I. I., Petoukhov, V., Stone, P. and Wang, Z. (2002). Earth system models of intermediate complexity: closing the gap in the spectrum of climate system models. *Climate Dynamics* 18(7), pp. 579–586.
- Cole, H., Henson, S., Martin, A. and Yool, A. (2012). Mind the gap: The impact of missing data on the calculation of phytoplankton phenology metrics. *Journal of Geophysical Research-Oceans* 117(C08030).

- Corbiere, A., Metzl, N., Reverdin, G., Brunet, C. and Takahashi, A. (2007). Interannual and decadal variability of the oceanic carbon sink in the North Atlantic subpolar gyre. *Tellus B*, 59, pp. 168–178.
- Cushing, D.H. (1990). Plankton production and year-class strength in fish populations: An update of the match mismatch hypothesis. *Advances in Marine Biology* 26, pp. 249–293.
- D’Ortenzio, F., Antoine, D., Martinez, E. and d’Alcalá, M.R. (2012). Phenological changes of oceanic phytoplankton in the 1980s and 2000s as revealed by remotely sensed ocean-color observations. *Global Biogeochemical Cycles* 26(GB4003).
- Dam, H.G., Miller, C.A. and Jonasdottir S.H. (1993). The trophic role of mesozooplankton at 47°N 20°W during the North Atlantic Bloom Experiment. *Deep-Sea Research Part II* 40 (1/2), pp. 197–212.
- Dandonneau, Y., Deschamps, P.Y., Nicolas, J.M., Loisel, H., Blanchot, J., Montel, Y., Thieuleux, F. and Bécu, G. (2004). Seasonal and interannual variability of ocean color and composition of phytoplankton communities in the North Atlantic, equatorial Pacific and South Pacific. *Deep-Sea Research Part II* 51(1–3), pp. 303–318.
- Doney, S.C., Lima, I., Moore, J. K., Lindsay, K., Behrenfeld, M.J., Westberry, T.K., Mahowald, N., Glover, D.M. and Takahashi, T. (2009). Skill metrics for confronting global upper ocean ecosystem-biogeochemistry models against field and remote sensing data. *Journal of Marine Systems* 76(1-2), pp. 95–112.
- Ducklow, H.W. (1989). Joint Global Ocean Flux Study: The 1989 North Atlantic Bloom Experiment. *Oceanography Magazine* 2, pp. 4–7.
- Dutkiewicz, S., Follows, S., Marshall, J. and Gregg, W.W. (2001). Interannual variability of phytoplankton abundances in the North Atlantic. *Deep-Sea Research Part II-Topical Studies in Oceanography* 48(10), pp. 2323 – 2344.
- Eby, M., Zickfeld, K., Montenegro, A., Archer, D., Meissner, K. J., and Weaver, A. J. (2009). Lifetime of anthropogenic climate change: millennial time scales of potential CO<sub>2</sub> and surface temperature perturbations. *Journal of Climate* 22, pp. 2501–2511.
- Edwards, M., and J. Richardson (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430, pp. 881–884.

- Egge, J. K., and Aksnes, D. L. (1992). Silicate as regulating nutrient in phytoplankton competition. *Marine Ecology Progress Series* 83(2–3), pp. 281–289.
- Evans, G.T. (2003). Defining misfit between biogeochemical models and data sets. *Journal of Marine Systems* 40, pp. 49–54.
- Fasham, M.J.R. and Pugh, P.R. (1976). Observations on the horizontal coherence of chlorophyll-*a* and temperature. *Deep-Sea Research* 23(6), pp. 527–538.
- Fox-Kemper, B., Ferrari, R. and Hallberg, R. (2008). Parameterization of mixed layer eddies. Part I: Theory and diagnosis. *Journal of Physical Oceanography* 38(6), pp. 1145–1165.
- Frank K.T., Perry, R.I. and Drinkwater, K.F. (1990). The predicted response of Northwest Atlantic invertebrate and fish stocks to CO<sub>2</sub>-induced climate change. *Transactions of the American Fisheries Society* 119, pp. 353–365.
- Gent, P.R. and McWilliams, J.C. (1990). Isopycnal mixing in ocean circulation models. *Journal of Physical Oceanography* 20, pp. 150–155.
- Gran, H. and Braarud, T. (1935). A quantitative study on the phytoplankton of the Bay of Fundy and the Gulf of Maine (including observations on hydrography, chemistry and morbidity). *Journal of the Biological Board of Canada* 1, pp. 219–467.
- Heinle, A. and Slawig, T. (2013). Impact of parameter choice on the dynamics of NPZD type ecosystem models. *Ecological Modelling* 267, pp. 93–101.
- Henson, S.A., Dunne, J.P. and Sarmiento, J.L. (2009). Decadal variability in North Atlantic phytoplankton blooms. *Journal of Geophysical Research* 114(C04013).
- Henson, S.A., Sanders, R., Madsen, E., Morris, P.J., Le Moigne, F. and Quartly, G.D. (2011). A reduced estimate of the strength of the ocean's biological carbon pump. *Geophysical Research Letters* 38(L04606).
- Holligan, P.M., Groom, S.B. and Harbour, D.S. (1993a). What controls the distribution of the coccolithophore, *Emiliania huxleyi*, in the North Sea? *Fisheries Oceanography* 2(3–4), pp. 175–183.
- Holligan, P.M., Fernandez, E., Aiken, J., Balch, W.M., Boyd, P., Burkill, P.H., Finch, M., Groom, S.B., Malin, G., Muller, K., Purdie, D.A., Robinson, C., Trees, C.C., Turner, S.M.,



and Vanderwal, P. (1993b). A biogeochemical study of the coccolithophore, *Emiliania huxleyi*, in the North Atlantic. *Global Biogeochemical Cycles* 7(4), pp. 879–900.

Ifremer French Research Institute for Exploration of the Sea (2013). Data Access. Available at: <http://www.ifremer.fr/cerweb/deboyer/mld/Data.php> [access date: 05.2013]

Climate Change 2007: The Physical Science Basis, Contribution of Working Group 1 to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, New York.

Keller, D.P., Oschlies, A., Eby, M. (2012). A new marine ecosystem model for the University of Victoria Earth system climate model. *Geoscientific Model Development Discussion* 5(2), pp. 1135–1201.

Krauss W., Doscher, R., Lehmann, A. and Viehoef, T. (1990). On eddy scales in the eastern and northern North Atlantic Ocean as a function of latitude. *Journal of Geophysical Research* 95, pp. 18049–18056.

Lampitt, R.S. (1985). Evidence for seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. *Deep-Sea Research Part I* 32, pp. 885–897.

Le Quéré, C., Harrison, S.P., Prentice, I.C., Buitenhuis, E.T., Aumont, O., Bopp, L., Claustre, H., Cunha, L.C.D., Geider, R.J., Giraud, X., Klaas, C., Kohfeld, K.E., Legendre, L., Manizza, M., Platt, T., Rivkin, R.B., Sathyendranath, S., Uitz, J., Watson, A.J. and Wolf-Gladrow, D. (2005). Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. *Global Change Biology* 11(11), pp. 2016–2040.

Le Quéré, C., Rodenbeck, C., Buitenhuis, E.T., Conway, T.J., Langenfelds, R., Gomez, A., Labuschagne, C., Ramonet, M., Nakazawa, T., Metzl, N., Gillett, N. and Heimann, M. (2007). Saturation of the Southern Ocean CO<sub>2</sub> sink due to recent climate change. *Science* 316(5832), pp. 1735–1738.

Leggett, R.W., Williams, L.R. (1981). A reliability index for models. *Ecological Modelling* 13, pp. 303–312.

Lévy, M. (2005). Nutrients in remote mode. *Nature* 437, pp. 628–631.

Loague, K., Green, R.E. (1991). Statistical and graphical methods for evaluating solute transport models: overview and application. *Journal of Contaminant Hydrology* 7, pp. 51–73.

- Lochte, K.; Ducklow, H.W.; Fasham, M.J.R., Stienen, C. (1993). Plankton succession and carbon cycling at 47°N 20°W during the JGOFS North Atlantic Bloom Experiment. *Deep-Sea Research Part II* 40(1–2), pp. 91–114.
- Longhurst, A.R. and Harrison, W.G. (1989). The biological pump: profiles of plankton production and consumption in the upper ocean. *Progress in Oceanography* 22(1), pp. 47–123.
- Longhurst, A., Sathyendranath, S., Platt, T. and Caverhill, C. (1995). An estimate of global primary production in the ocean from satellite radiometer data. *Journal of Plankton Research* 17(6), pp. 1245–1271.
- Mahadevan, A., D'Asaro, E., Lee, C., Perry, M.J. (2012). Eddy-Driven Stratification Initiates North Atlantic Spring Phytoplankton Blooms. *Science* 337(6090), pp. 54–58.
- Mann, K.H., Lazier, J.R.N. (2006). Dynamics of Marine Ecosystems: biological-physical interactions in the oceans. 3<sup>rd</sup> ed. Dartmouth: Blackwell Publishing.
- Marshall, S.M., Orr, A.P. (1928). The photosynthesis of diatom cultures in the sea. *Journal of Marine Biological Association* 15, pp. 321–364.
- Martinez, E., Antoine, D., D'Ortenzio, F., Boyer Montégut, C. de Boyer (2011). Phytoplankton spring and fall blooms in the North Atlantic in the 1980s and 2000s. *Journal of Geophysical Research-Oceans* 116(C11029).
- McKinley, G.A., Follows, M.J., Marshall, J. (2004). Mechanisms of air–sea CO<sub>2</sub> flux variability in the equatorial Pacific and the North Atlantic. *Global Biogeochemical Cycles* 18(2), GB2011.
- Meissner, K.J., Weaver, A.J., Matthews, H.D. and Cox, P.M. (2003). The role of land surface dynamics in glacial inception: a study with the UVic Earth system model. *Climate Dynamics* 21, pp. 515–537.
- Moore, J.K., Doney, S.C. and Lindsay, K. (2004). Upper ocean ecosystem dynamics and iron cycling in a global 3-D model. *Global Biogeochemical Cycles* 18(4), GB4028.
- Nanninga, H.J. and Tyrrell, T. (1996). Importance of light for the formation of algal blooms by *Emiliania huxleyi*. *Marine Ecology Progress Series* 136(1–3), pp. 195–203.

- Nash, J.E., Sutcliffe, J.V. (1970). River flow forecasting through conceptual models, part 1 — a discussion of principles. *Journal of Hydrology* 10, pp. 282–290.
- National Oceanography Center (2013). Data Overview. Available at: <http://www.eurosites.info/data.php> [access date: 05.2013]
- National Oceanography Data Center (2013). World Ocean Atlas 2009 Data in NetCDF format. Available at: [http://www.nodc.noaa.gov/OC5/WOA09/netcdf\\_data.html](http://www.nodc.noaa.gov/OC5/WOA09/netcdf_data.html) [access date: 04.2013]
- Oschlies, A. and Garcon, V. (1998). Eddy-induced enhancement of primary production in a model of the North Atlantic Ocean. *Nature* 394, pp. 266–269.
- Pingree R.D., Holligan, P.M., Mardell, G.T. and Head, R.N. (1976). The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic Sea. *Journal of the Marine Biological Association of the United Kingdom* 56(4), pp. 845–873.
- Platt, T., Fuentes-Yaco, C. and Frank, K. (2003). Spring algal bloom and larval fish survival. *Nature* 423, pp. 398–399.
- Platt, T., Sathyendranath, S., White, G.N., Fuentes-Yaco, C., Zhai, L., Devred, E. And Tang, C. (2010). Diagnostic Properties of Phytoplankton Time Series from Remote Sensing. *Estuaries and Coasts* 33(2), pp. 428–439.
- Rahmstorf, S. (1996). On the freshwater forcing and transport of the Atlantic thermohaline circulation. *Climate Dynamics* 12(12), pp. 799–811.
- Redfield, A.C. (1934). On the proportions of organic derivatives in seawater and their relation to the composition of plankton. In *James Johnstone Memorial Volume*, edited by: Daniel, R.J., University of Liverpool, pp. 176–192.
- Richardson, A.J. and Schoeman, D.S. (2004). Climate impact on plankton ecosystems in the northeast Atlantic. *Science* 305, pp. 1609–1612.
- Ross, O.N., Sharples, J. (2007). Phytoplankton motility and the competition for nutrients in the thermocline. *Marine Ecology Progress Series* 347, pp. 21–38.

- Sabine, C.L., Feely, R.A., Gruber, N., Key, R.M., Lee, K., Bullister, J.L., Wanninkhof, R., Wong, C.S., Wallace, D.W.R., Tilbrook, B., Millero, F.J., Peng, T.-H., Kozyr, A., Ono, T., Rios, A.F. (2004): The Oceanic Sink for Anthropogenic CO<sub>2</sub>. *Science* 305, pp. 367–371.
- Sarmiento, J.L., Slater, R., Barber, R., Bopp, L., Doney, S.C., Hirst, A.C., Kleypas, J., Matear, R., Mikolajewicz, U., Monfray, P., Soldatov, V., Spall, S.A., Stouffer, R. (2004). Response of ocean ecosystems to climate warming. *Global Biogeochemical Cycles* 18(3), GB3003.
- Sasaoka, K., S. Chib Savidge G., Turner, D.R., Burkhill, P.H., Watson, A.J., Angel, M.V., Pingree, R.D., Leach, H. and Richards, K.J. (1992). The BOFS 1990 spring bloom experiment: Temporal evolution and spatial variability of the hydrographic field. *Progress in Oceanography* 29, pp. 235-281.
- Schmittner, A., Oschlies, A., Matthews, H.D. and Galbraith, E. D. (2008). Future changes in climate, ocean circulation, ecosystems, and biogeochemical cycling simulated for a business-as-usual CO<sub>2</sub> emission scenario until year 4000 AD. *Global Biogeochemical Cycles*. 22(1), GB1013.
- Sharples, J., Ross, O., Scott, B., Greenstreet, S. and Fraser, H. (2006). Inter-annual variability in the timing of stratification and the spring bloom in the North-western North Sea. *Continental Shelf Research* 26, pp. 733–751.
- Siegel, D., S. Doney, and J. Yoder (2002a). The North Atlantic spring phytoplankton bloom and Sverdrup's Critical Depth Hypothesis. *Science* 296 (5568), 730–733.
- Signorini, S.R., Häkkinen, S., Gudmundsson, K., Olsen, A., Omar, A.M., Olafsson, J., Reverdin, G., Henson, S.A., McClain, C.R. and Worthen, D.L. (2012). The role of phytoplankton dynamics in the seasonal and interannual variability of carbon in the subpolar North Atlantic – a modeling study. *Geoscientific Model Development* 5(3), pp. 683–707.
- Simmons, H.L., Jayne, S.R., St. Laurent, L.C. and Weaver, A.J. (2004). Tidally driven mixing in a numerical model of the ocean general circulation. *Ocean Modelling* 6(3–4), pp. 245–263.
- Sommer, U. (1994). The impact of light-intensity and daylength on silicate and nitrate competition among marine phytoplankton. *Limnology and Oceanography* 39(7), pp. 1680–1688.

- Stow, C.A., Roessler, C., Borsuk, M.E., Bowen, J.D., Reckhow, K.H. (2003). A comparison of estuarine water quality models for TMDL development in the Neuse River Estuary. *Journal of Water Resources Planning and Management* 129, pp. 307–314.
- Stow, C.A., Jolliff, J., McGillicuddy, D.J., Doney, S.C., Allen, J.I., Friedrichs, M.A.M., Rose, K.A. and Wallheadg, P. (2009). Skill assessment for coupled biological/physical models of marine systems. *Journal of Marine Systems* 76(1-2), pp. 4–15.
- Stramska, M., Dickey, T.D., Marra, J., Plueddermann, A., Langdon, C. and Weller, R. (1995). Bio-optical variability associated with phytoplankton dynamics in the North Atlantic Ocean during spring and summer 1991. *Journal of Geophysical Research-Ocean* 100(C4), pp. 66621–66632.
- Sverdrup, H. (1953). On conditions for the vernal blooming of phytoplankton. *ICES Journal of Marine Science* 18, pp. 287–295.
- Takahashi, T., Takahashi, T.T., Sutherland, S.C. and Williams, R.G. (1995). An Assessment of the Role of the North Atlantic as a CO<sub>2</sub> Sink. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 348(1324), pp. 143-152.
- Takahashi, T., Sutherland, S. C., Sweeney, C., Poisson, A., Metzl, N., Tilbrook, B., Bates, N., Wanninkhof, R., Feely, R. A., Sabine, C., Olafsson, J., and Nojiri, Y. (2002). Global sea-air CO<sub>2</sub> flux based on climatological surface ocean pCO<sub>2</sub>(2), and seasonal biological and temperature effects. *Deep-Sea Research Part II* 49, 1601–1622.
- Takahashi, T., Sutherland, S.C., Wanninkhof, R., Sweeney, C., Feely, R.A., Chipman, D.W., Hales, B., Friederich, G., Chavez, F., Sabine, C., Watson, A., Bakker, D.C.E., Schuster, U., Metzl, N., Yoshikawa-Inoue, H., Ishii, M., Midorikawa, T., Nojiri, Y., Kortzinger, A., Steinhoff, T., Hoppema, M., Olafsson, J., Arnarson, T.S., Tilbrook, B., Johannessen, T., Olsen, A., Bellerby, R., Wong, C.S., Delille, B., Bates, N.R. and de Baar, H.J.W. (2009). Climatological mean and decadal change in surface ocean pCO<sub>2</sub>, and net sea-air CO<sub>2</sub> flux over the global oceans. *Deep-Sea Research Part II- Topical Studies in Oceanography* 56(8–10), pp. 554–577.
- Taucher, J. and Oschlies, A. (2011). Can we predict the direction of marine primary production change under global warming? *Geophysical Research Letters* 38(L02603).

- Taylor, J.R. and Ferrari, R. (2011). Ocean fronts trigger high latitude phytoplankton blooms. *Geophysical Research Letters* 38(23), L23601.
- Thomas, L.N. and Taylor, J.R. (2010). Reduction of the usable wind-work on the general circulation by forced symmetric instability. *Geophysical Research Letters* 37, L18606.
- Townsend D.W., Keller, M.D., Sieracki M.E. and Ackleson S.G. (1992). Spring phytoplankton blooms in the absence of vertical water column stratification. *Nature* 360, pp. 59-62.
- Townsend, D.W., Cammen, L.M., Holligan, P.M., Campbell, D.E. and Pettigrew, N.R. (1994). Causes and consequences of variability in the timing of spring phytoplankton blooms. *Deep Sea Research Part I* 41(5/6), pp. 747–765.
- Waniek, J.J. (2003). The role of physical forcing in initiation of spring blooms in the northeast Atlantic. *Journal of Marine Systems* 39, pp. 57–82.
- Ward, B.A. and Waniek, J.J. (2007). Phytoplankton growth conditions during autumn and winter in the Irminger Sea, North Atlantic. *Marine Ecology Progress Series* 334, pp. 47–61.
- Watson, A.J., Robinson, C., Robinson, J.E., Williams, P.J.L.B. and Fasham M.J.R. (1991). Spatial Variability in the sink for atmospheric carbon-dioxid in the North Atlantic. *Nature* 350, pp. 50-53.
- Weaver, A.J., Eby, M., Wiebe, E.C., Bitz, C.M., Duffy, P.B., Ewen, T.L., Fanning, A.F., Holland, M.M., Mac Fadyen, A., Matthews, H.D., Meissner, K.J., Saenko, O., Schmittner, A., Wang, H.X. and Yoshimori, M. (2001): The UVic Earth System Climate Model: Model Description, Climatology and Applications to Past, Present and Future Climates. *Atmosphere-Ocean* 39(4), pp. 361–428.
- Winder, M., and J. E. Cloern (2010). The annual cycles of phytoplankton biomass. *Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences*, 365(1555), pp. 3215–3226.
- Yamada, K., and Wolf, K.U. and Woods, J.D. (1988). Lagrangian simulation of primary production in the physical environment- -the deep chlorophyll maximum and nutricline: a theory on biological-physical interactions in the world ocean. *Academic Publishers, Dordrecht*, pp. 5-7

Yoder, J.A., McClain, C.R., Feldman, G.C. and Esaias, W.E. (1993). Annual cycles of phytoplankton chlorophyll concentrations in the global ocean: a satellite view. *Global Biogeochemical Cycles* 7, pp. 181–193.

Yool, A., Popova, E.E. and Anderson, T.R. (2011). MEDUSA-1.0: a new intermediate complexity plankton ecosystem model for the global domain. *Geoscientific Model Development* 4(2), pp. 381–417.